

Anatomy, phylogeny and taxonomy of the gadoid fish genus *Macruronus* Günther, 1873, with a revised hypothesis of gadoid phylogeny

GORDON J. HOWES

Department of Zoology, British Museum (Natural History), Cromwell Rd, London, SW7 5BD

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SYNOPSIS. The osteology and other anatomical features of *Macruronus* and *Merluccius* are compared; particular differences are in the structure of cranial, infraorbital, suspensorial, opercular and pelvic bones and in the vertebral column, caudal fin structure and dorsal body musculature. Presumed synapomorphies relating *Macruronus* and *Merluccius* are shown to be homoplastic. *Macruronus*, *Lyconus* and possibly *Lyconodes* form a monophyletic group recognised as family Macruronidae; *Merluccius* is the sole member of Merlucciidae. Macruronidae is considered a basal member of a monophyletic assemblage of families termed 'higher' gadoids; Merlucciidae is considered the derived sister lineage to Gadidae. The taxonomy of Macruronidae is reviewed.

INTRODUCTION

The subject of this paper is the phylogenetic position of the genus *Macruronus* which presently contains five species. Two species; *M. novaezelandiae* and *M. magellanicus* are of economic importance in the Southern Ocean and are commonly known as southern hakes, blue grenadiers or hoki in

New Zealand waters and as merluza de cola around Chile and Argentina. The genus *Macruronus* is considered to belong to the family Merlucciidae along with the genera *Merluccius*, *Lyconus* and *Lyconodes*. Norman (1966) was the first author to regard *Macruronus* and *Steindachneria* as merlucciids which he assigned to a separate subfamily (Macruroninae); until then both genera had been considered as macrouroids.

Marshall (1966) identified characters suggesting unity of the Merlucciidae which also included the poorly known

Lyconus and *Lyconodes*. Marshall & Cohen (1973) removed *Steindachneria* to a monotypic family leaving four genera in the Merlucciidae. *Merluccius*, because of its economic importance, has been well-studied and Inada (1981) produced a taxonomic revision of the species, reviewed their ecology and gave detailed osteological descriptions. Inada's work has been used for anatomical comparison.

No anatomical study of *Macruronus* has been made, although Regan (1903) remarked on some osteological features. He stated that *Macruronus* was, in its cranial morphology, exactly like *Merluccius* observing that '... this correspondence extends to minute structural details, the upper surface of the skull being precisely similar in both ...' Regan's view persuaded Norman (1937) to include *Macruronus* and *Merluccius* in the same family.

Regan's observations are not borne out by the present study. There are few, other than superficial and plesiomorphic resemblances between *Macruronus* and *Merluccius*. *Lyconus* (and possibly *Lyconodes*), however, are closely related to *Macruronus* (p. 101).

These findings have led to taxonomic changes in genera comprising the Merlucciidae, to a reappraisal of the polarities of certain characters used in gadoid classification and to a revised hypothesis of gadoid phylogenetic relationships.

MATERIALS AND METHODS

The anatomical descriptions of *Macruronus* are based on specimens of three lots of *M. magellanicus*; BMNH 1936.8.26:342–351, size range, 130–250mm TL (including a cleared and alizarin/alcian stained specimen); 1936.8.26:358–363, 440–450mm TL and 1936.8.26:358–363, 700–780mm TL (including skeletal specimens); *M. novaezealandiae*; unregistered skeleton, ca 160mm TL. Specimens of *M. novaezealandiae* examined: 1895.4.26:1–4, 120–150mm TL and unregistered, 520mm TL. Radiographs of these specimens were used for vertebral counts.

Cleared and stained specimens, skeletons and alcohol preserved material of species representing all gadoid families have been used for comparison; details of these specimens are listed in Howes (1988). The register numbers of specimens used for the illustrations are given in the respective captions.

Abbreviations used in the figures

Unless otherwise stated, the scale bars in the figures are in mm divisions. For ease of comparison, the terms used by Inada are given in brackets.

aa	anguloarticular (angular)
aap	premaxillary articular process
ac	actinost
add	<i>erector + depressor analis</i> muscle
ahy	anterohyal (ceratohyal)
ans	'accessory' neural spine
ap	premaxillary ascending process
ar	anal fin ray
ard	anal fin radial
asp	autosphenotic (sphenotic)
av	abdominal vertebra (numbered)
bb	basibranchial (numbered)
bh	basihyal

bo	basioccipital
bof	basioccipital facet
br	branchiostegal ray
cc	cartilaginous core of exoccipital condyles
cb	ceratobranchial (numbered)
cfr	caudal fin rays
cl	cleithrum
cm	coronomeckelian bone
co	coracoid
cv	caudal vertebra (numbered)
de	dentary
dfc	diagonal frontal crest (posterior wall of sensory canal)
dh	dorsohyal (upper hypophyal)
dr	dorsal fin ray
drd	dorsal fin radial
ds	dermosphenotic
eb	epibranchial (numbered)
ect	ectopterygoid
edd	<i>erector + depressor dorsalis</i> muscle
ent	entopterygoid
epo	epioccipital (epiotic)
epu	epural
epx	<i>epaxialis</i> muscle
esa	anterior extrascapular (supratemporal)
esp	posterior extrascapular (supratemporal)
exf	exoccipital articulatory facet
exo	exoccipital
fIX	foramen for glossopharyngeal nerve
fX	foramen for vagus nerve
fc	frontal canal
fd	<i>flexor dorsalis</i> muscle
fds	<i>flexor dorsalis superioris</i> muscle
fr	frontal
fth	foramen for trigeminal and hyomandibularis nerves
fv	<i>flexor ventralis</i> muscle
fvi	<i>flexor ventralis inferioris</i> muscle
hb	hypobranchial (numbered)
hk	head kidney
hl	<i>hypochordal longidorsalis</i> muscle
hmf	hyomandibular fossa
hs	haemal spine
hsh	hypural segment of hypaxial muscle
hy	hypural (numbered)
hyo	hyomandibular
hyx	<i>hypaxialis</i> muscle
ic	intercalar
icv	intercalated vertebra
ihy	interhyal
io	interorbital (numbered)
iop	interopercular
ird	<i>interradialis</i> muscle
imp	intermuscular process of hyomandibular
lb	Baudelot's ligament
le	lateral ethmoid
lew	lateral ethmoid wing
lfc	lateral frontal crest
lia	interneural arch ligament
lip	interopercular-preopercular ligament
liv	intervertebral ligament
ls	<i>lateralis superficialis</i> muscle
mc	Meckel's cartilage
me	mesethmoid
mec	mesethmoid cartilage
met	metapterygoid

mfc medial frontal cavity (mucuous cavity)
 na nasal
 nac neural arch
 nll lateral line nerve
 nns2 second neural spine nerve
 ns neural spine (numbered)
 nX vagus nerve
 op opercular
 oph opercular process of hyomandibula
 pa parietal
 pah parhypural
 pal palatine
 pb pelvic bone
 pbb pharyngobranchial; numbered (pharyngeal)
 pbp postpelvic process
 pc postcelithrum
 pcr procurrent caudal ray
 phy posterohyal (epihyal)
 pmp postmaxillary process of the premaxilla
 poh preopercular process of hyomandibula
 pop preopercular
 pp parapophyses
 pr pleural rib
 pro prootic

ps parasphenoid
 psm parasphenoid medial process
 psp parasphenoid ascending process
 pte pterotic
 pts pterosphenoid
 ptt posttemporal
 pu preural vertebra; numbered
 qu quadrate
 ra retroarticular
 re rostrodermosupraethmoid (mesethmoid)
 rt replacement tooth
 sb swimbladder
 sc scapular
 scl supracleithrum
 so supraoccipital
 sop subopercular
 sy symplectic
 tp tooth patch
 tse transverse septum
 u ural centrum; numbered
 vh ventrohyal (lower hypohyal)
 vo vomer (prevomer)
 X X-bone (dorsal radial)
 Y Y-bone (anal radial)

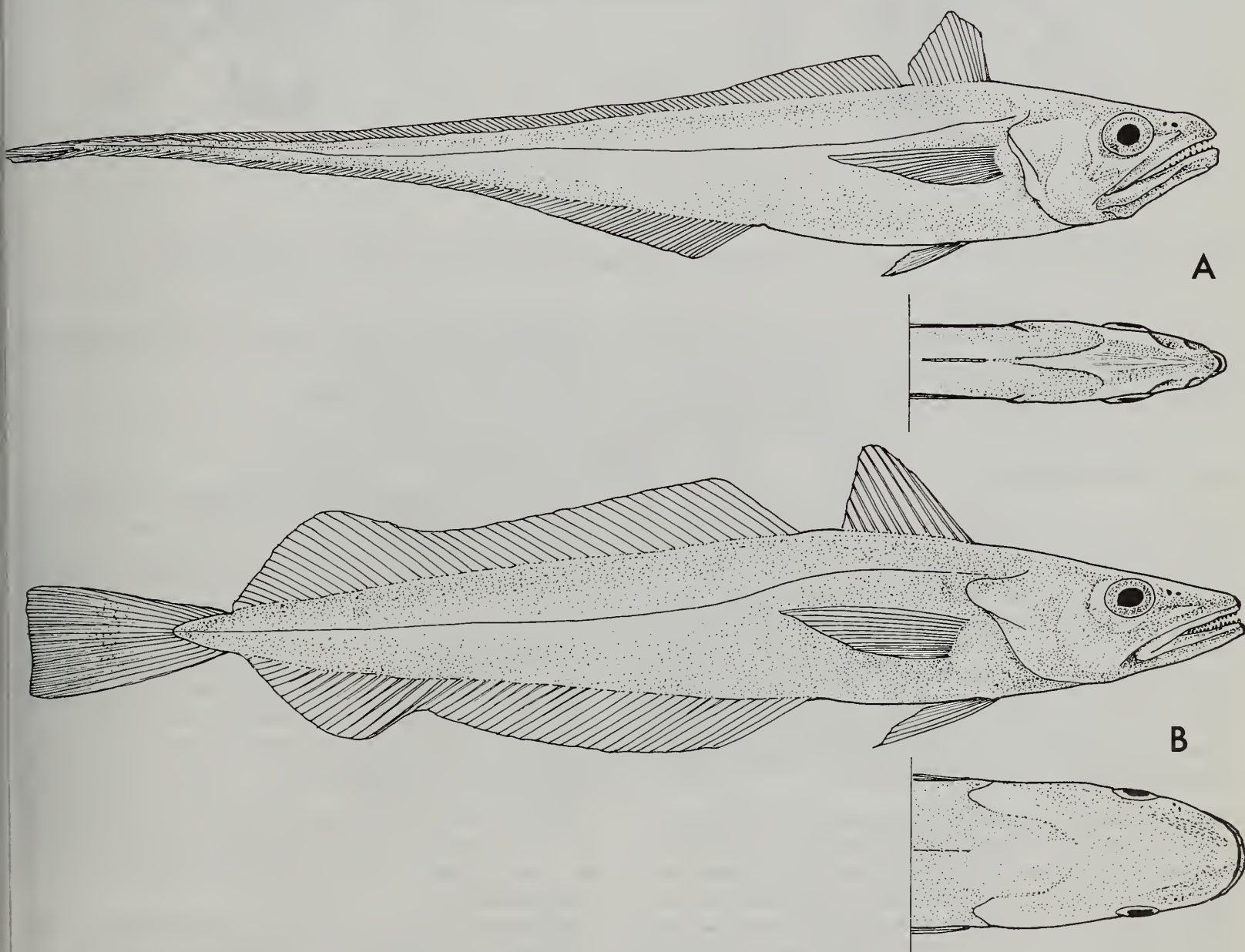


Fig. 1 A. *Macruronus magellanicus*; B. *Merluccius merluccius*, both showing the lateral aspect of the fish with dorsal views of the head region. Drawn from specimens (A) BMNH 1936.8.26: 342–351, 205mm TL, (B) 1963.5.14: 118, 280mm TL.

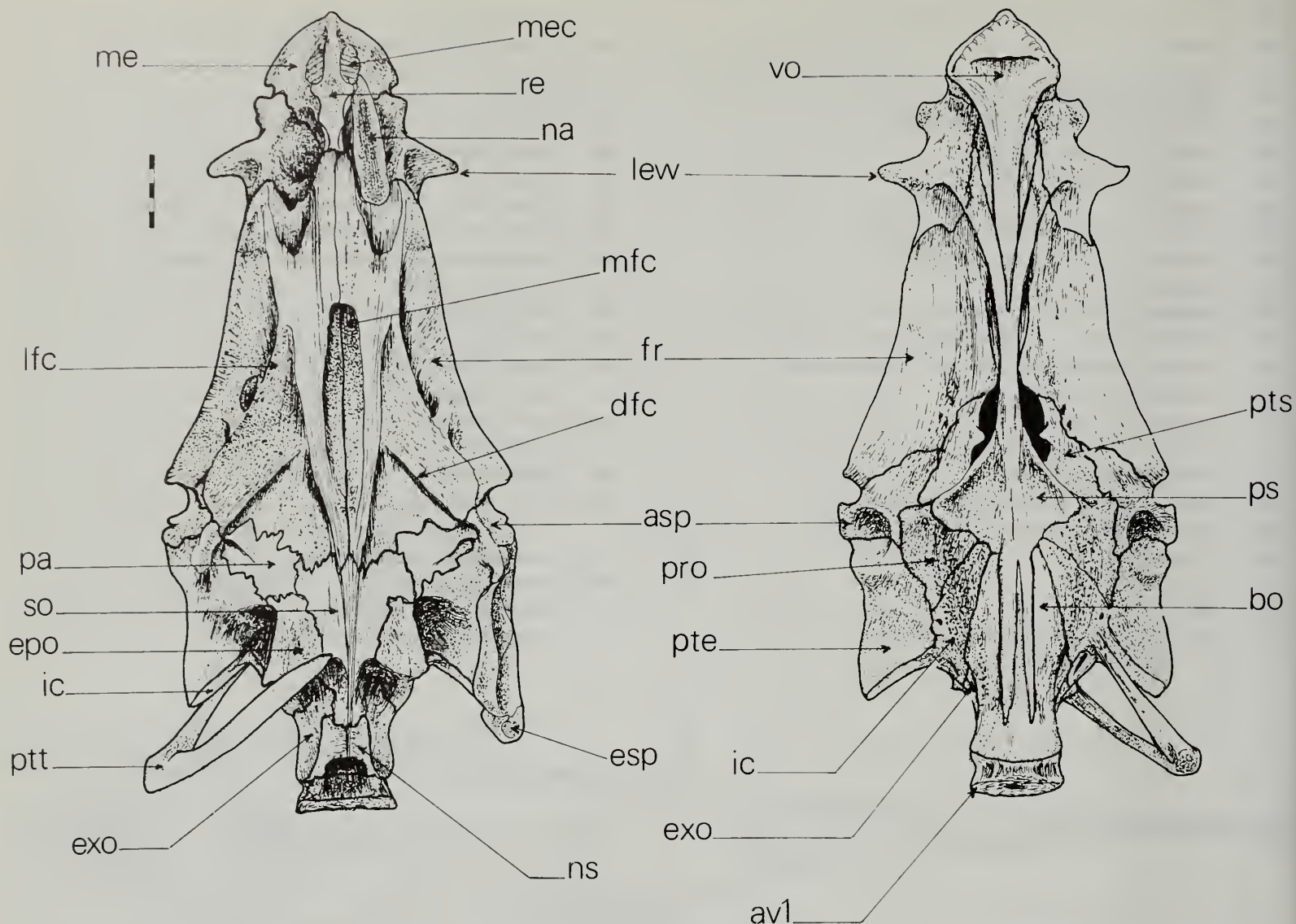


Fig. 2 *Macruronus magellanicus*, neurocranium in (left) dorsal and (right) ventral views. BMNH 1936.8.26: 352-7 (skeleton).

ANATOMY OF MACRURONUS AND COMPARISON WITH MERLUCCIUS

External morphology (Fig. 1)

Macruronus: Body elongate, strongly compressed with tapered tail. Two dorsal fins separated by slight gap; first short-based, the second confluent with caudal fin. Pectoral fins situated high, level with centre of eye; pelvic origin below or somewhat posterior to pectoral origin. Anal fin extends along posterior half of body and either confluent with, or separated by indentation from, caudal fin rays. Upper caudal rays often extended. Head relatively short (16.6-19.5% TL), jaws oblique, snout short. Opercular border not attenuated and closely attached to body wall. Scales thin and deciduous. Blue coloration.

Merluccius: Body moderately compressed with typical symmetrical gadoid tail. Two dorsal fins, the second with posterior rays extended, not confluent with caudal fin. Pectoral fins low on body, level with lower border of eye. Pelvic origin anterior to pectoral. Anal fin with posterior rays extended and not confluent with caudal fin. Head long (24.4-33.5% SL), jaws straight or slightly oblique, lower jaw projecting, snout long. Operculum with attenuated, un-

restricted, posterior border. Scales thin and deciduous, ellipsoidal. Silver coloration.

Cranium (Figs 2-9)

Cranial shape:

Macruronus; characterized by cranial depth, relatively short otic and occipital regions and anteriorly tapered roof. *Merluccius*; cranium depressed, particularly where frontals meet ethmoid region; otic and occipital regions elongate, cranial roof nearly oblong. Detailed differences are:

1. Ethmoid region:

Macruronus (Figs 2 & 3). Dorsal ethmoid surface (rostrodermosupraethmoid) narrow and cruciform, sloping ventrally at 45° with ethmoid bloc (mesethmoid) separated from vomer by shallow cartilage. Lateral ethmoid short with concave laminate outer margin, ventrally produced into strong triangular lateral process. Vomer thick, arrow-shaped, ventral surface crossed transversely by deep recess; single row of incurved, unicuspid teeth on either side (7-8 in *M. magellanicus*; 12-15 irregularly arranged in *M. novaezealandiae*).

Merluccius (Figs 5A,C). Rostrodermosupraethmoid thick, only anterior part slopes ventrally (at an angle of 65°), cruciform part remaining horizontal. Lateral ethmoid long, outer margin thick, straight, with slight ventral lateral

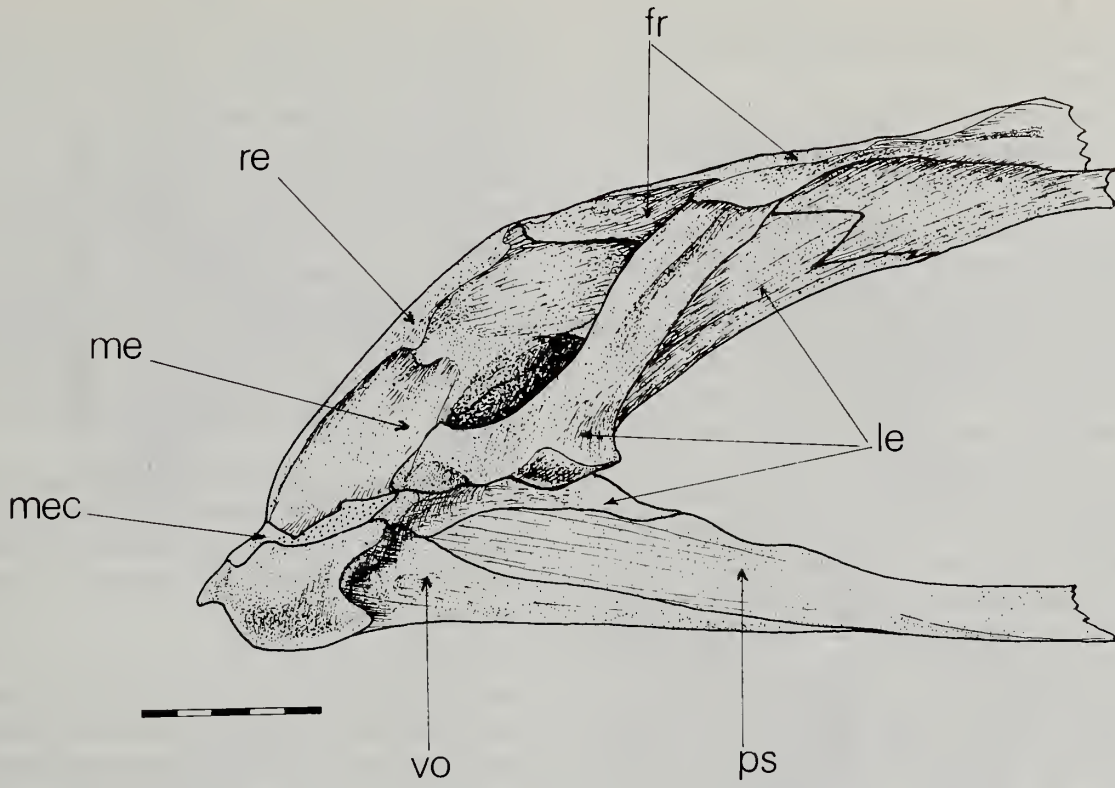


Fig. 3 *Macruronus magellanicus*, ethmoid region in lateral view (same specimen as in Fig. 2).

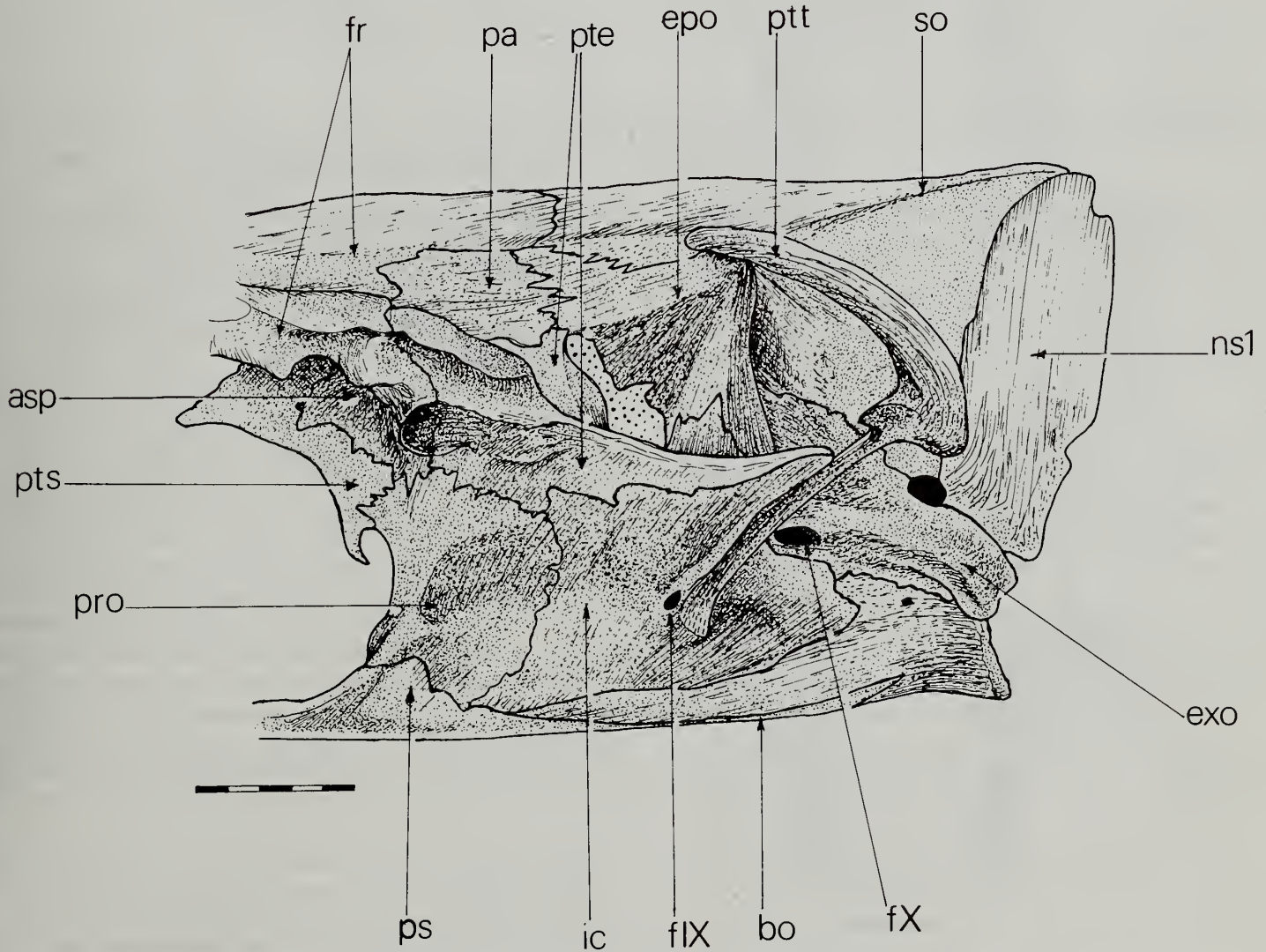


Fig. 4 *Macruronus magellanicus*, otic and occipital part of neuro-cranium in lateral view (same specimen as in previous figures).

process. Vomer thin, bluntly triangular with dependent rim of thin bone; two rows of long incurved teeth on either side, 12–16 in outer, 6–7 in inner row.

In both genera nasals equally developed as long, shallow troughs of thin bone situated on either side of ethmoid.

2. Orbital region:

Macruronus (Figs 2;4). *Frontals* broadly triangular, each with irregular and indented anterior border. Posterolaterally, frontal contacts dermosphenotic which lies in a notch formed partly by the frontal margin. Bony channel of frontal sensory canal broad with an extensive anterior opening communicating with nasal. There are two lateral openings, the anterior one opens by a medial foramen into a central cavity. The broad, canopy-like roof covering frontal canal rises dorso-medially as a strong crest which continues rising posteriorly to meet its partner anterior to their junction with supraoccipital. Frontals sink between the crests forming deep V-shaped central cavity (so-called mucous cavity). Posteromedially, frontal surface forms sloped platform between high medial crest and diagonal crest which provides posterior wall of sensory canal. Ventrally, frontals bear medially curved, converging lamina which form an open groove for olfactory tracts. *Parietals* are short and broad, without crests.

Pterosphenoid small, oblong with short, somewhat medially curved, ventral processes which forms a dorsomedial support for trigeminal nerve tract (Fig. 4).

Parasphenoid circular in cross-section, narrow in orbital

region but deepening anteriorly where it meets lateral ethmoids; the shallow, long ascending processes curves outward to meet prootic, intercalar and basioccipital (Fig. 4).

Merluccius has subrectangular frontals with gently convex margins above lateral ethmoids (Fig. 5). A strong crest runs diagonally from anterolateral margin to join its partner on the supraoccipital, forming a broad V. Medial wall of supra-orbital (frontal) canal formed by short crest (wrongly termed the 'suborbital' by Inada, 1981), which runs parallel to the frontal margin and divergent to central frontal crest to become confluent with pterotic crest. Ventral laminae extend from the anterior part of each frontal and run parallel to one another. Parietals long and narrow in some species (Inada, 1981).

Pterosphenoid similar in size and shape to that of *Macruronus* but ventrally meets ascending process of parasphenoid and lower rim of prootic; parasphenoid square in cross section, with flat ventral surface, anteriorly it rises gently to meet lateral ethmoids.

3. Otic region:

Macruronus (Fig. 4). *Autosphenotic* small with strut-like lateral surface, ventrally indented with major part of hyomandibular fossa. Dorsally only small area of autosphenotic contributes the cranial surface, lying laterally between frontal and pterotic. Lateral border concave and, with the curved margin of the frontal forms a deep notch which accommodates a small, thimble-like *dermosphenotic* (see also p. 102).

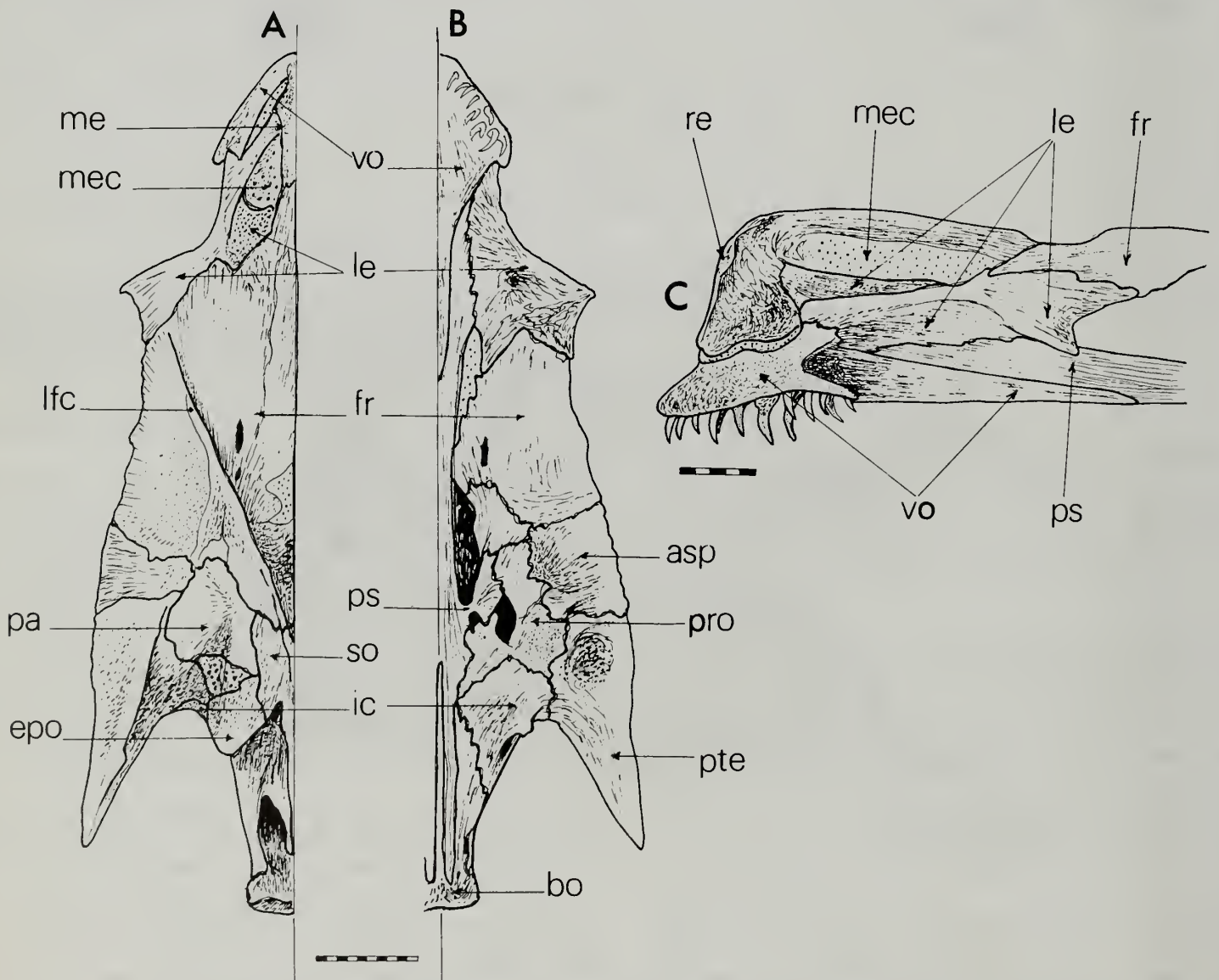


Fig. 5 *Merluccius merluccius*, neurocranium in A, dorsal and B, ventral views. C, ethmoid region in lateral view. BMNH Uncat. skeleton.

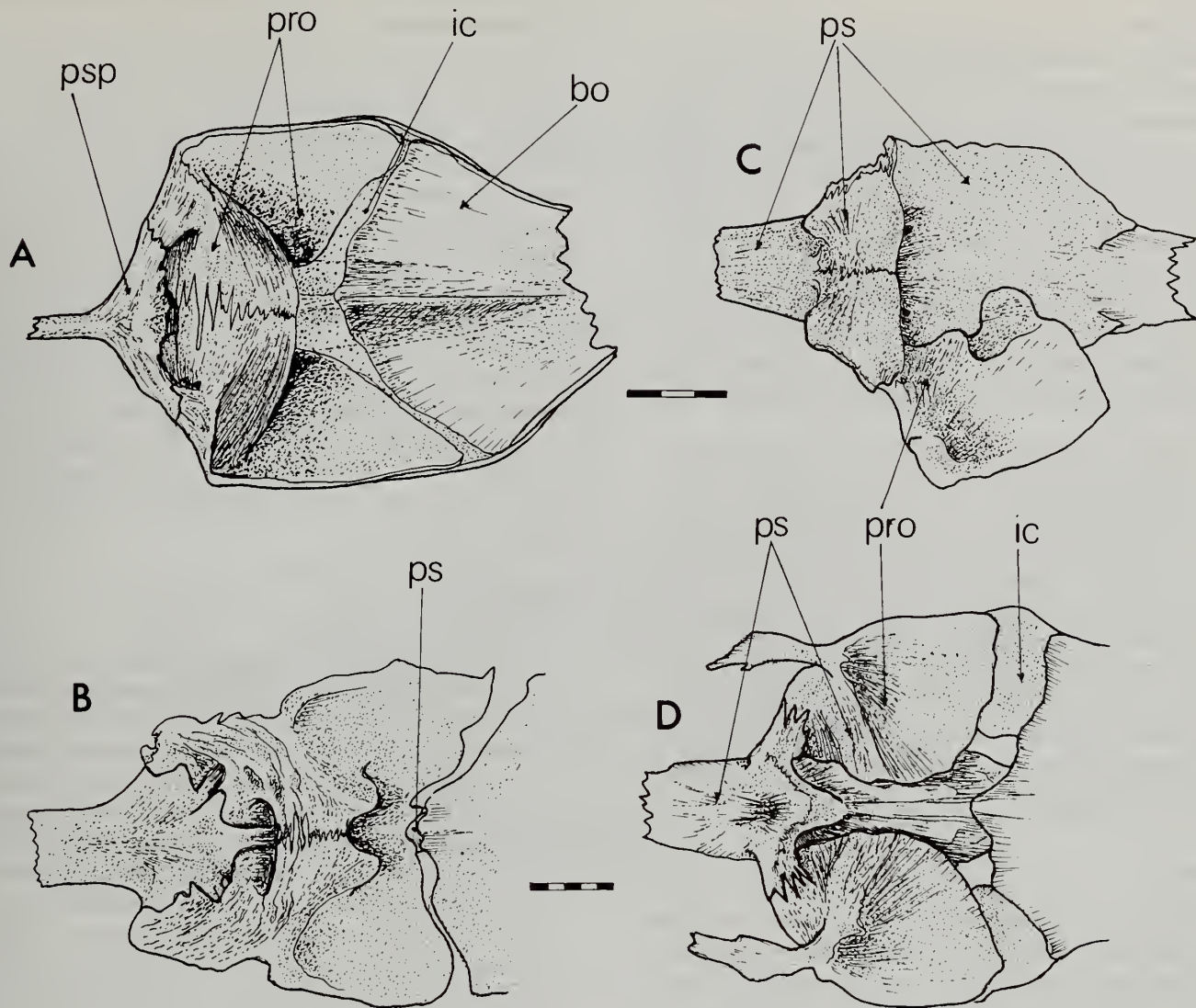


Fig. 6 Dorsal views of the cranial floor of A, *Macruronus magellanicus* (BMNH 1936.8.26: 352-7); B, *Merluccius merluccius*; C, *Mora moro*; D, *Merlangius merlangus*. (B-C from Ford collection of unregistered skeletal material).

Pterotic shallow but broad; posterolaterally meets intercalar and together they form a broad, slightly outwardly directed wing. Pterotic bears anterolaterally part of hyomandibular fossa; anterodorsally its roof bears a ridge forming the medial wall of the sensory canal which runs across its dorsoposterior region. Large area of cartilage separates medial border of pterotic from epioccipital wherein is formed the *posttemporal fossa*.

Prootic short and deep, medial margin thickened. Anteroventrally, at junction with parasphenoid ascending process, its wall is greatly thickened and extends medially to contact that of opposite side, forming a thick transverse bony septum with a convex posterior face. Anterior face of septum indented at ventral midline by shallow fossa but there is no posterior opening into the cranial cavity (Fig. 6).

Intercalar large, rising posteriorly to form laterally directed wing, posterior margin of which continues ventrally as a ridge down body of bone; anterior to base of ridge is the glossopharyngeal nerve foramen, posterior to which is the process which supports the posttemporal limb. Medially, the intercalar rises as a thin bony margin to the exoccipital (Figs 6 & 9).

Merluccius has a larger autosphenotic which presents a much greater exposed area between frontal and pterotic (Fig. 5A). Pterotic bears a larger portion of hyomandibular fossa than in *Macruronus* and, unlike that taxon, forms the entire posterolateral cranial wing. Posteromedially pterotic is

deeply depressed but the cartilage separating it from the epioccipital is not as extensive and consequently the posttemporal fossa is not as deep as in *Macruronus*.

Prootic more inflated and notched or perforated by foramen for trigeminal nerve trunk (Fig. 8). The size and shape of foramen variable; in some specimens it perforates prootic wall, in others it indents margin; anterior rim of foramen provided by pterosphenoid (see Inada, 1981:71-2 for an illustrated account of variability). As in *Macruronus* each prootic is joined to its partner across the midline by a transverse bony extension. However, the extension is shelf-like with a concave posterior margin and does not contact the prootic floor thus leaving a tunnel through which run the rectus muscles (Fig. 6).

Intercalar has more extensive contact with parasphenoid, and extends further ventrally and posteriorly than in *Macruronus*. Most noticeably, it does not form the posterior boundary of the lateral cranial wing (Fig. 8).

Saccular otolith: Macruronus (Fig. 7). Otolith thin and oblong with squared-off rostrum and irregularly rounded caudal margin. Its medial surface convex, ostium and cauda broad and shallow, containing small colliculi. Saccular otolith of *Merluccius* differs in elongate, oval outline, entire crenulate dorsal margin and narrower ostium and cauda. The hyaline-zone features of the *M. novaezelandiae* otolith have been described and used in age determination by Kuo & Tanaka (1984d).

4. Occipital region:

Macruronus (Fig. 9). *Epioccipital*, tall, semi-pyramidal with depressed cartilaginous medial face, posttemporal articulates with its dorsoposterior surface. *Exoccipital* shallow, containing in its anteroventral margin a large foramen for vagus nerve. Posteriorly, paired condyles extend and curve slightly downward on either side of foramen magnum. *Basioccipital* shallow anteriorly, flooring most of the posterior part of cranium; meets parasphenoid ventrally along a narrow V-shaped groove. *Supraoccipital* with moderately developed median crest and steeply-sloped sides meeting parietals and exoccipitals. Posteriorly, crest extends as a thin lamina gripped between the anteriorly extended halves of first neural spine.

Occipital region of *Merluccius* differs in several respects from that of *Macruronus* (Figs 6 & 8). *Epioccipital* is shorter and broader; *exoccipital* shallower and larger with an almost horizontal crest terminating in the articular condyle with vagus nerve foramen situated in lateral centre of bone. *Basioccipital* posteriorly longer than that of *Macruronus* but terminates anteriorly below intercalar-posttemporal process whereas that of *Macruronus* extends anteriorly. *Supraoccipital* longer and broader with more acutely sloped crest. According to Inada (1981:68), although there is variability in crest height among *Merluccius* species it is not sufficient to indicate specific identity.

Posttemporal

Macruronus (Fig. 9). Broad V-shaped element with thin arched horizontal limb attaching proximally to epioccipital; limb's distal surface forms facet which articulates with supracleithrum. Ventral limb also narrow, lies adnate to sloped, free border of intercalar to articulate with slight posterolateral process as base of intercalar border. *Merluccius* has narrowly V-shaped posttemporal (Fig. 8), its upper limb straight and broadly expanded where it articulates with supracleithrum; ventral limb thin and separated from posterior margins of pterotic and intercalar. Unlike *Macruronus* both upper and lower limbs of the posttemporal are aligned in nearly the same vertical plane so that the lower arm is displaced both posteriorly and medially from the pterotic-intercalar wing.

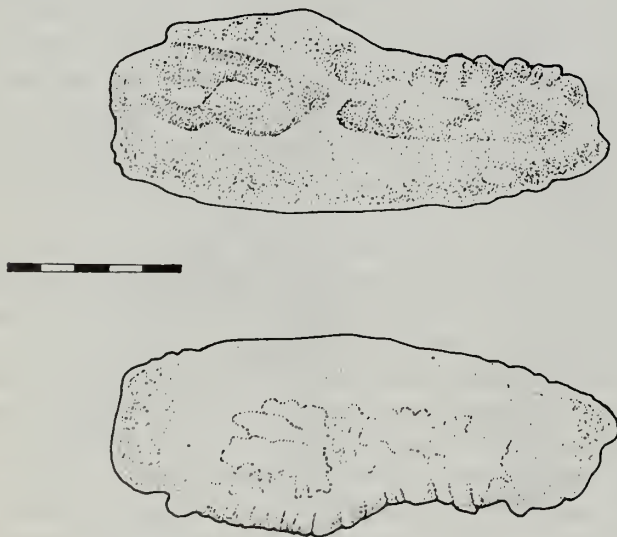


Fig. 7 Sagittal otolith (from left side of cranium) of *Macruronus magellanicus* (BMNH 1936.8.26: 358–363), showing (above) medial and (below) lateral faces; anterior is toward the left.

Extrascapulars

Extrascapulars (supratemporals) are four in *Macruronus* and *Merluccius*. In *Macruronus* all are confined to lateral margin of the cranium, above the pterotic (Figs 2 & 9); in *Merluccius* two extrascapulars lie medially along inner side of horizontal posttemporal limb. In *Macruronus* the posterior extrascapular is circular with a dorsolateral flange, that preceding is long and oblong covered only by skin; above and anterior to it lies the largest of the four, having a narrow dorsolateral flange abutting the anterior element which lies above the sphenotic and communicates directly with the frontal branch of supraorbital canal. The space between first and third extrascapulars occupied by band of thick connective tissue running from medial surface of large second element to attach to pterotic rim. In *Macruronus* it seems the large, third extrascapular has moved laterally with respect to that in *Merluccius*.

Infraorbitals

Macruronus (Fig. 10) has six infraorbitals; 1st elongate with, halfway along its length, a shallow ascending process which articulates with lateral surface of lateral ethmoid wing; 2nd infraorbital triangular, posteriorly expanded where it meets the 3rd which is almost square, occupying the corner of the series; 4th small, circular with deep outer flange covering sensory canal; 5th elongate, boomerang-shaped with sensory canal entirely enclosed. Unlike the other infraorbitals, this bone is densely ossified with a solid posterior flange.

Merluccius has five infraorbitals (Inada, 1981). Most noticeable differences are taller articular process of 1st infraorbital which articulates with ventral surface of the lateral ethmoid wing; deeper and smaller 2nd infraorbital; larger 3rd and 4th, and smaller 5th. All infraorbitals are partially covered along their orbital borders by an ossified flange leaving the remainder of the infraorbital sensory canal covered only by skin (the usual condition among gadoids). Only in *Macruronus* and *Lyconus* is the sensory canal of 5th infraorbital completely enclosed (condition in *Lyconodes* unknown).

Upper and lower jaws (Figs 11 & 12)

Macruronus has relatively short upper jaw. *Premaxilla* with tall ascending and articular processes and short, rounded postmaxillary process. Two rows of teeth, outer row 16–17, long, medially curved; inner row *ca* 35, minute, lying flat and medially directed, the last *ca* 10 being evenly spaced, others irregular. *Maxilla* has tall articular head with a broad, deep, medially directed process; posterodorsal process rises gently from halfway along the bone and has vertical posterior margin separated by short distance from distal tip of the maxilla. Maxillary tip with slight ventroposterior prolongation.

Merluccius has a long upper jaw. *Premaxilla* with short, sloped ascending process and long-based articular process; postmaxillary process tall, backwardly sloped. Two rows of teeth, those of inner series almost same length as those of outer and are recurved and depressible. Inada (1981) stated that there are 40–50 teeth on each side, possibly referring to total numbers of inner and outer row teeth. However, in *Merluccius merluccius* examined there are 27–30 in both outer and inner rows (total of *ca* 60). *Maxilla* has low articular head with a broad, shallow, medially directed process; posterodorsal process indicated only by a slight posterior elevation of

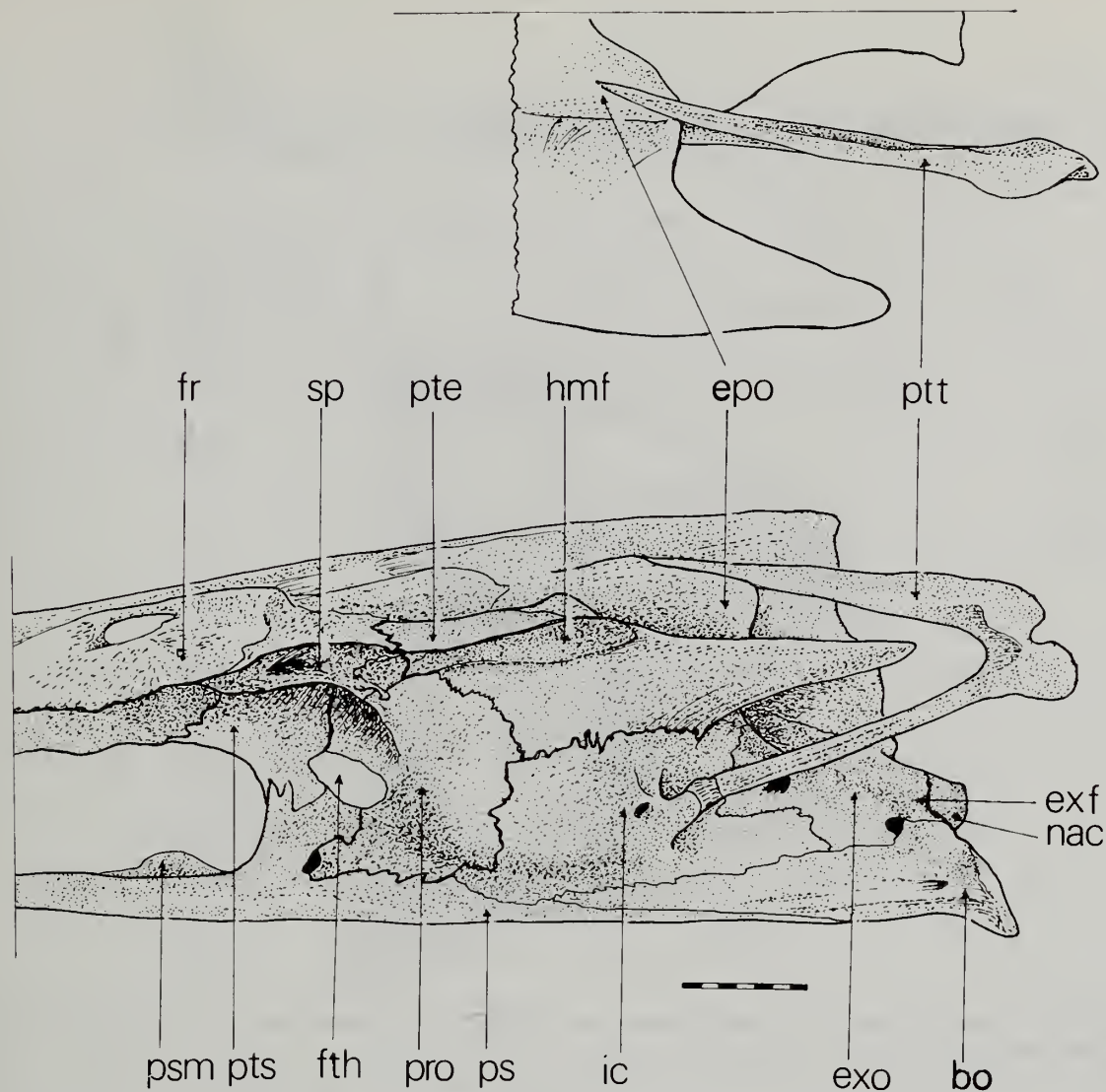


Fig. 8 *Merluccius productus*, otic and occipital part of neurocranium in lateral view; above, dorsal view of the posttemporal showing its near parallel alignment with the midline, cf. Fig. 2. (BMNH 1896.9.25: 6, skeleton, ex: Stanford University Collection).

the bone and its concave posterior margin. Distal tip of maxilla triangular to truncate, directed ventrally.

Lower jaw of *Macruronus* short and deep; *dentary* with deep anterior cavity housing mandibularis section of *adductor mandibulae* muscle; posterior border of cavity vertical. Single row of 15–20 long, widely spaced teeth. *Anguloarticular* has sloped dorsoposterior border with a tall articular condyle, its anterior vertical margin narrowly separated from dentary. *Retroarticular* L-shaped, its horizontal, ventral part extending forward along ventrolateral margin of dentary for almost a third of that bone's length (Fig. 12A).

Lower jaw of *Merluccius* long and shallow, dentary with long anterior mandibularis cavity, but with a sloped posterior border. Teeth in two series; Inada (1981) gives a count of 30–40 for the outer row. In *Merluccius merluccius* examined there are 30–33 outer and 30–40 inner teeth. *Retroarticular* is wedge-shaped element lying medial to posteroventral corner of anguloarticular (Fig. 12B). In both *Macruronus* and *Merluccius* the coronomeckelian cartilage is well-developed but the coronomeckelian bone is a minute element lying on its dorsoposterior surface. An anteroventrally extended retroarticular similar to that of *Macruronus* occurs elsewhere in gadoids only in *Lyconus*.

Labial ligament (Howes, 1988:8) well-developed, extending from anterolateral face of dentary to attach to distal surface of maxilla (Howes, 1988, fig. 17). In *Merluccius* labial ligament also well-developed but stems from mid-lateral face of dentary.

Suspensorium

Macruronus (Fig. 13). *Palatine* elongate with narrow anterior premaxillary prong; ventrally indented with deep fossa from which originates anterior part of the *adductor mandibulae* A1b muscle; medially contacts lateral process of mesethmoidal portion of the lateral ethmoid (Howes, 1987: fig. 3A). *Ectopterygoid* deep and folded laterally along its length so forming deep gutter contiguous with ventral depression of palatine; posteriorly forked, one arm extending ventrally along quadrate's medial border as far as its condyle, other, shorter arm extends posterodorsally to lie medial to metapterygoid. *Entopterygoid* large, medially sloped, contacting parasphenoid along its dorsal border; posteriorly narrowly separated from hyomandibular. *Metapterygoid* small, triangular, its apex extends dorsally to meet anterior lamina of hyomandibular. *Quadrate* fan-shaped with deep posteroventral extension which articulates medially with *symplectic*. Latter elongate with an expanded dorsal head narrowly separated by a band of cartilage from the hyomandibular stem.

Hyomandibular long with a concave dorsal border, articular process rod-like and accommodated by sphenotic fossa. Opercular process relatively short, lying below dorsal level of the bone. Foramen for hyomandibular branch of facial nerve perforates anterior lamina and is exposed laterally. Entire length of posterior border of hyomandibular stem contacts preoperculum.

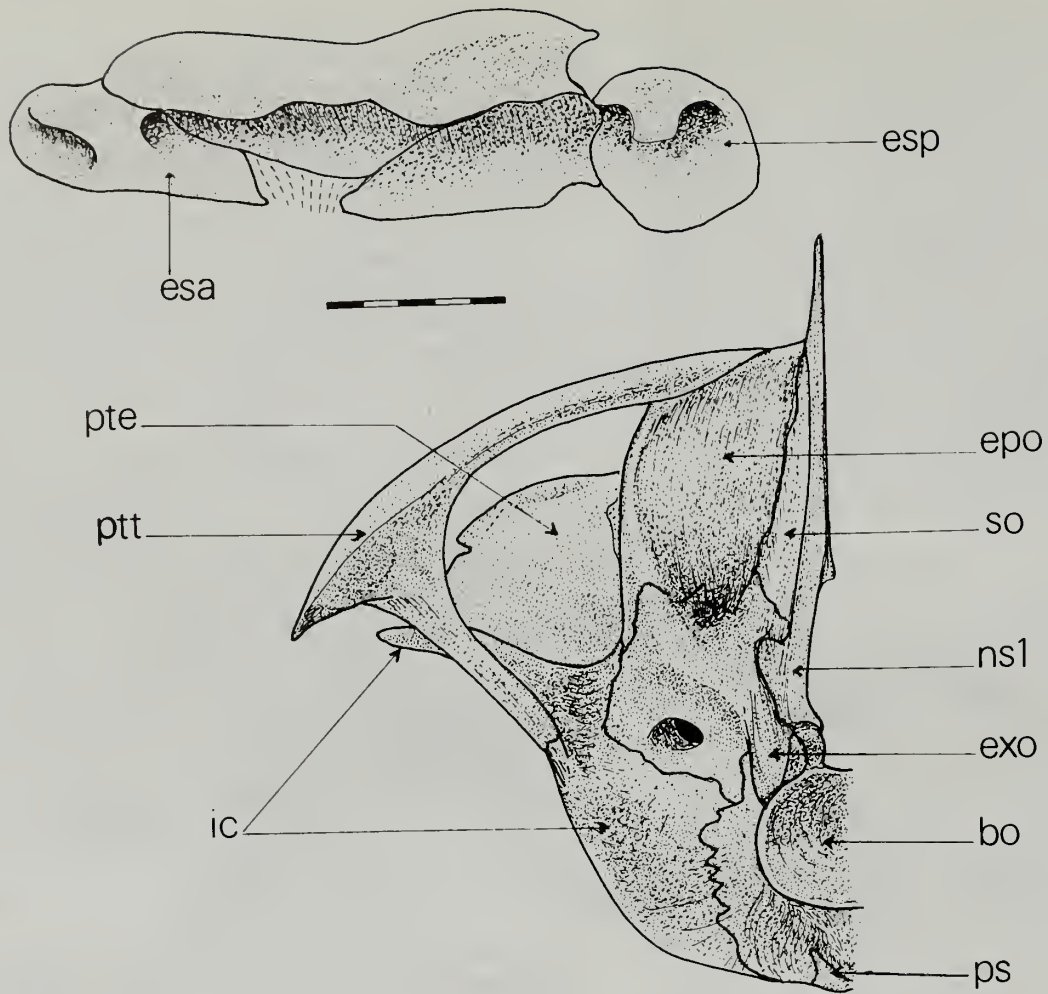


Fig. 9 *Macruronus magellanicus*, posterior view of neurocranium and posttemporal, and (above) lateral view of the extrascapular series of the left side. (BMNH 1936.8.26: 352-7.)

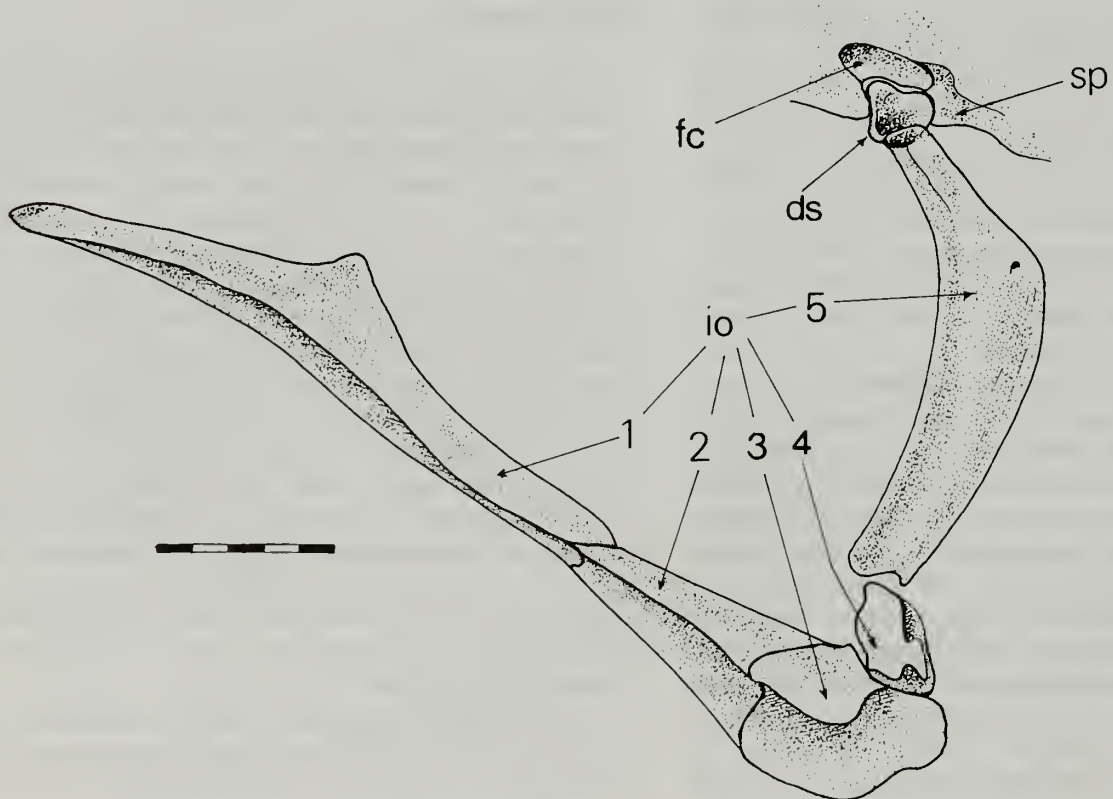


Fig. 10 *Macruronus magellanicus*, infraorbital series (BMNH 1936. 8.26: 352-7).

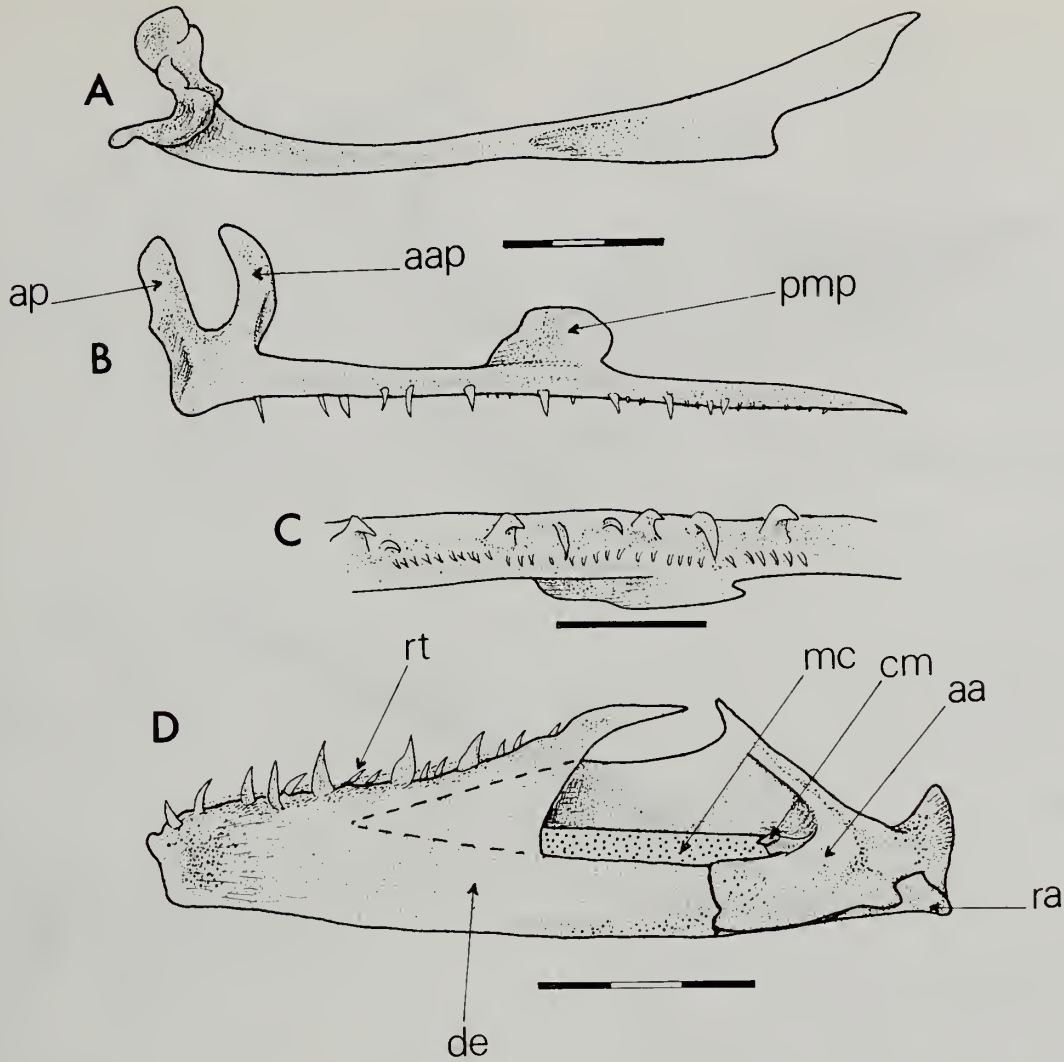


Fig. 11 *Macruronus magellanicus*, jaw bones. A, maxilla in dorsal view; B, premaxilla in lateral view; C, ventral view of the region of the premaxilla below the postmaxillary process showing double row of teeth; D, medial view of the lower jaw. A-C, BMNH 1936.8.26: 352-7 (skeleton); D, 1936.8.26: 342-56 (alcian-alizarin stained preparation).

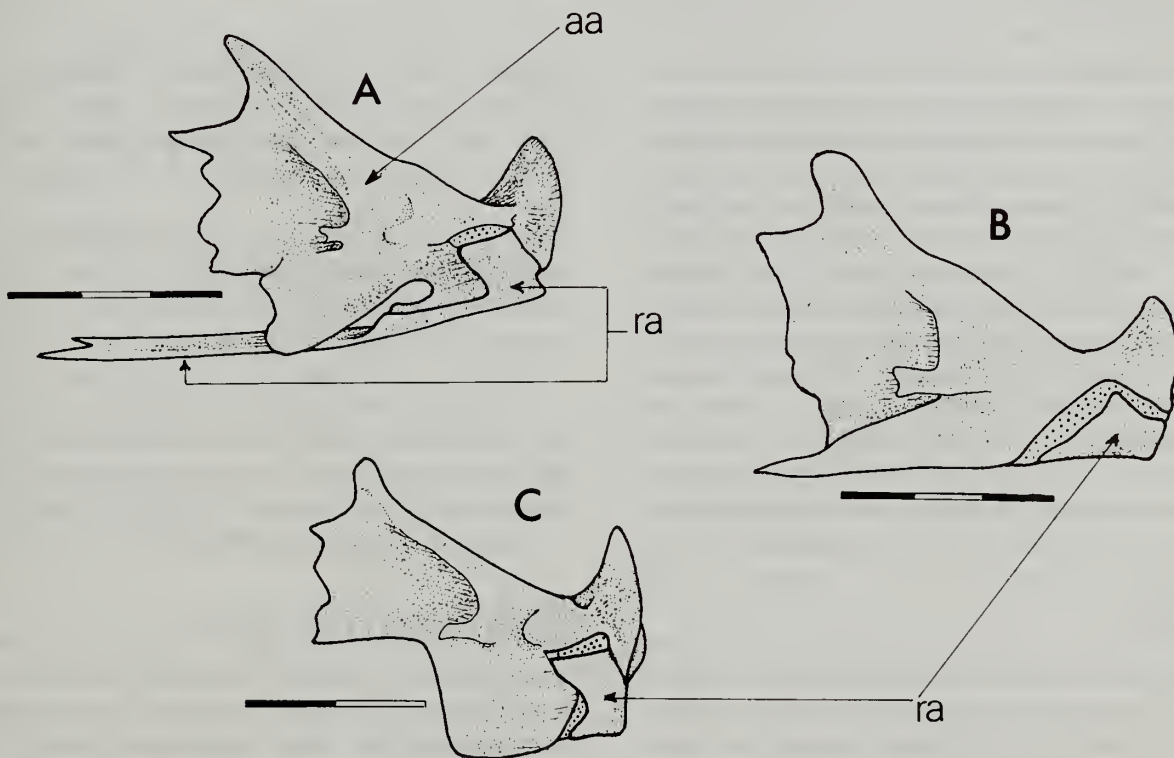


Fig. 12 Posterior region of the lower jaws, in medial views of; A, *Macruronus magellanicus* (BMNH 1936.8.26: 342-56); B, *Merluccius merluccius* (1971.7.21: 44-57); C, *Steindachneria argentea* (1963.2.25: 344-54). All alcian-alizarin stained preparations (the coronomeckelian cartilage has been omitted).

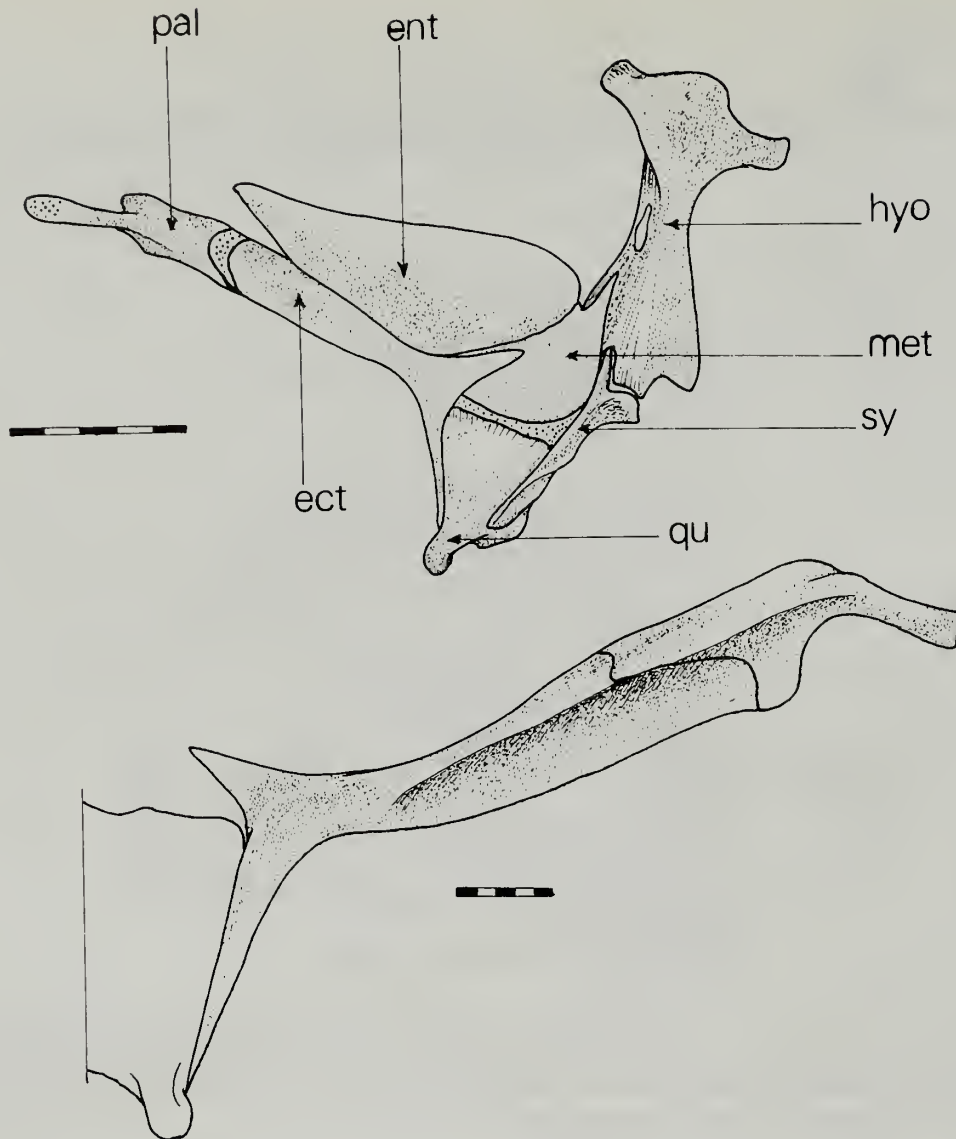


Fig. 13 *Macruronus magellanicus*, suspensorium and palato-ptyergoid series. Above, medial aspect (BMNH 1936.8.26: 342–56, alcian-alizarin stained preparation); below, lateral view of palatine and ectopterygoid (1936.8.26: 358–63, skeleton).

The suspensorial elements of *Merluccius* differ in several respects from those of *Macruronus*: Palatine is deeper posteriorly, bearing a shallow lateral depression for the origin of *adductor mandibulae* A1b; ectopterygoid not extending as far ventrally along quadrate border and not posteriorly forked; entopterygoid not as extensive nor meeting metapterygoid (Inada, 1981:76); symplectic short and oblong; metapterygoid's posterior border extends further dorsally along hyomandibular limb; hyomandibular has deep cranial articularity and long opercular processes. The most notable feature of the *Merluccius* hyomandibular, lacking in *Macruronus*, is a broad, lateral flange bearing two ventrally directed processes (Fig. 14A). Inada (1981) found significant enough differences in the size of the anterior (intermuscular) process to recognise two species groups of *Merluccius*.

Opercular bones

Macruronus (Fig. 15A) has a deep *interopercular* with an extended anterior tip; dorsomedially is a shallow articular facet with which articulates the interhyal; posterior border vertical. Extensively broad ligament joins interopercular to medial face of preopercular. *Preopercular* deep with long upright part, medially bearing a pronounced process which articulates with symplectic cartilage. *Opercular* broadly tri-

angular with a well-developed horizontal medial ridge. *Subopercular* broadly triangular with rounded borders contacting opercular and preopercular, overlapped extensively by latter. An interopercular-subopercular ligament is absent.

Merluccius differs most noticeably from *Macruronus* in interopercular morphology (Figs 15B & 16C). The bone's anterior tip is blunter, its posterior border subtriangular and extended; dorsomedial articular surface highly developed with a thick rim acting as a stop to the posterior movement of the interhyal. Interopercular-preopercular ligament narrow, also a narrow interopercular-subopercular ligament. Subopercular oblong with straight posterior border contacting opercular with only narrow portion of anterior margin being overlapped by preopercular. Opercular with strong medial ridge.

Hyoid arches (Fig. 16A)

There are only minor differences between the hyoid bar elements of *Macruronus* and *Merluccius*. In *Macruronus* *anterohyal* deeper and shorter but *posterohyal* somewhat longer than in *Merluccius*. Two last *branchiostegal rays* of *Macruronus* more expanded and spathiform than those of *Merluccius* (Fig. 16C); in both genera the posterohyal supports one branchiostegal.

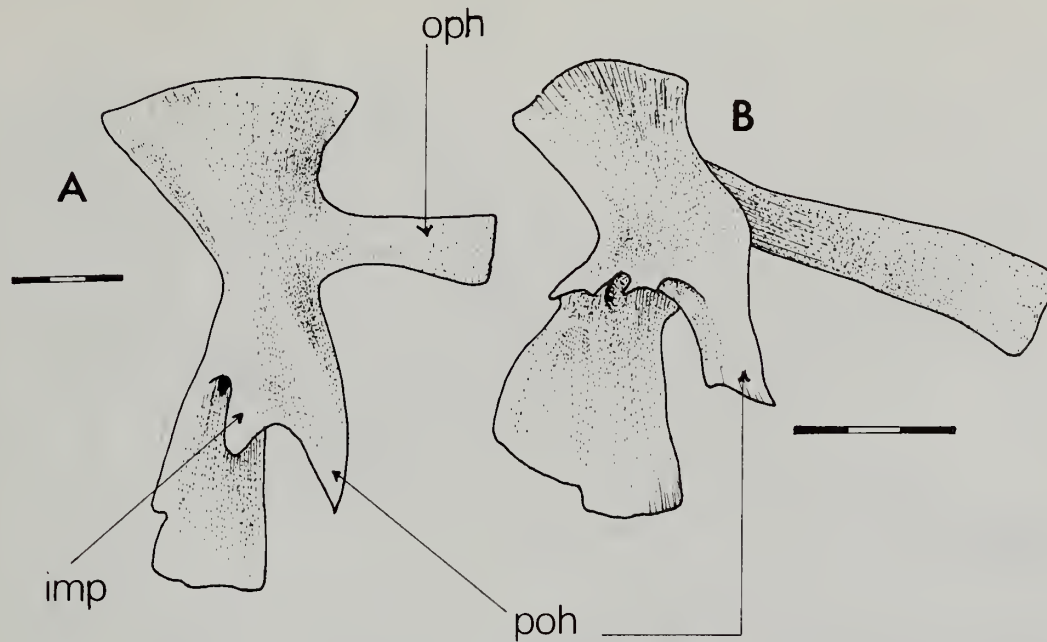


Fig. 14 Hyomandibular, in lateral views of A, *Merluccius productus* (BMNH 1896.9.25: 6) and B, *Microgadus proximus* (1890.11.15: 237), to show lateral shelf, discussed on p. 101.

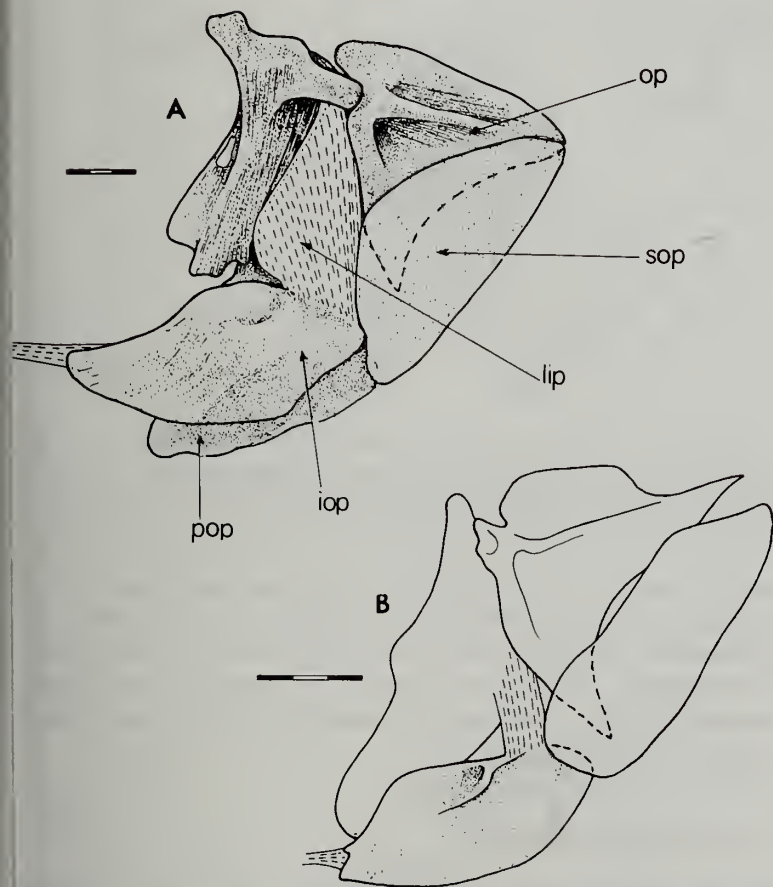


Fig. 15 Opercular series, medial views of A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–56); B, *Merluccius merluccius* (1976.8.30: 87–96), alcian-alizarin stained preparations.

Urohyal is significantly different in the two taxa; that in *Macruronus* has an extended, rod-shaped anterodorsal (basibranchial) process (Fig. 16B). The basibranchial process of *Merluccius* urohyal is a fan-shaped plate (Fig. 16C) which more closely resembles urohyal shape of other gadoids; in other gadoid taxa, however, the urohyal basibranchial process is merely a continuation of the vertical median plate or keel of the bone and is not distinctly separated as in *Merluccius* (see Fig. 16C, also Inada, 1981, fig. 36, cf.

Kusaka, 1974, figs 176–184 of various gadoids including *Macruronus*).

Branchial arch

Macruronus differs from *Merluccius* in several respects in the lower branchial arch elements (Fig. 17).

Macruronus has three median elements, an elongate, dumbbell-shaped *basihyal*, a small cartilaginous 1st *basibranchial* articulating with the 2nd hypobranchials, an elongate, ossified 2nd *basibranchial* articulating with 3rd hypobranchials, and a minute, cartilaginous 3rd *basibranchial* lying at posterior tip of 2nd *basibranchial*. Between 4th *ceratobranchials* a tough ligament stretches from 3rd *basibranchial*, bifurcates and attaches to both 5th *ceratobranchials*. The 3rd hypobranchial is elongate with ventrally curved medial border; posteriorly it articulates with both 3rd and 4th *ceratobranchials*, both bearing elongate tooth-plates.

Merluccius has a relatively short rod-shaped *basihyal*, a long cartilaginous *basibranchial* articulating with 1st and 2nd hypobranchials and a short, arrow-head shaped *basibranchial* articulating with broadly triangular 3rd hypobranchials (Inada, 1981).

Macruronus has 9 long, denticulate *gill-rakers* on 1st hypobranchial, *Merluccius* has 3–10 small, denticulate tubercular rakers. Both genera have elongate *cerato-* and *hypobranchials*, the outer *ceratobranchials* of *Macruronus* bearing 14–15 rakers, those of *Merluccius* 11–12. Like other gadoids, *Macruronus* has two rows of rakers on all arches, those on inner surfaces of 1st and outer and inner surfaces of 2nd–4th hypo- and *ceratobranchials*, short, flat and spinose; those on inner margins of the elements transversely arranged, with their broadest face directed anteriorly (Fig. 18A). In *Merluccius*, *gill-rakers* on inner side of 1st arch and subsequent arches are small, tubercular and spinose but arranged so their broadest face is directed along *ceratobranchial* axis; below and surrounding the base of each raker may be one to six small denticulate patches (Fig. 18B; Inada, 1981, figs 47 & 48).

Upper branchial elements in *Macruronus* comprise four rather short *epibranchials*, all with tall, uncinat processes

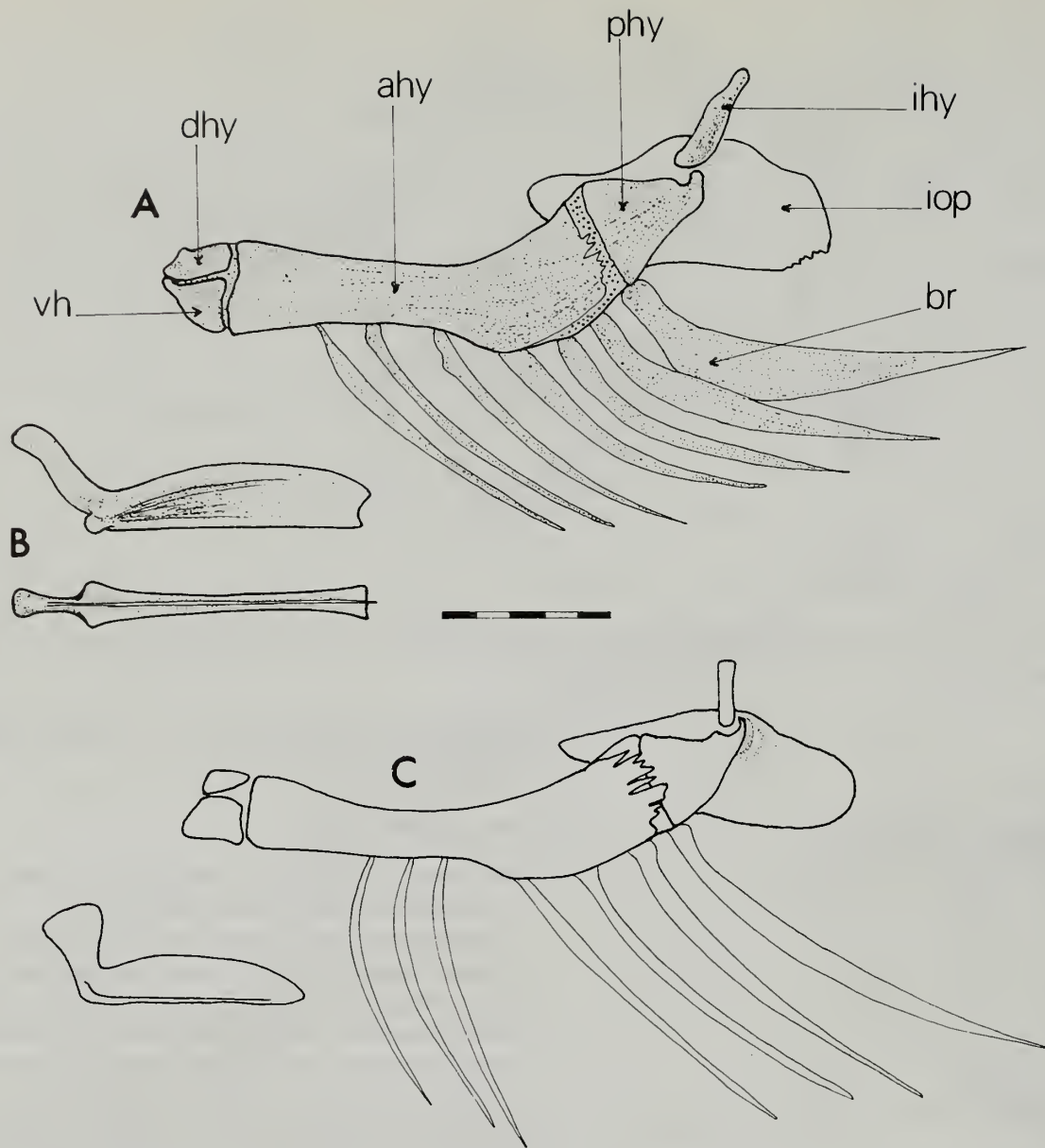


Fig. 16 Hyoid arch elements of; A & B, *Macruronus magellanicus* (BMNH 1936.8.26: 342–56), and C, *Merluccius merluccius* (1971.7.21: 44–47), alcian-alizarin stained preparations. The hyoid bar in A is shown in medial view, the urohyal in B & C in lateral and (B) dorsal views.

and three *pharyngobranchials* (numbers 1–3). Pharyngobranchial 1 is cartilaginous; pharyngobranchial 3 bears three struts which articulate with the 2nd, 3rd and 4th epibranchials; pharyngo-branchial 2 articulates with the 1st epibranchial; *interarcual cartilage* absent. There are 8 slender, denticulate gill-rakers on outer surface of 1st epibranchial and 2 or 3 flat, denticulate rakers on inner surface. Similar rakers occur on 3rd and 4th epibranchials. Tooth patches are present on 3rd epibranchial and pharyngobranchials 2 and 3.

In *Merluccius* epibranchial uncinata processes are lower than in *Macruronus* and the struts of pharyngobranchial 3 are longer and prominently curved mesad. Inada (1981) and Patterson & Rosen (1989) report pharyngobranchial 1, but there is no interarcual cartilage. Tooth patches are present on pharyngobranchial 2 and 3 and on 3rd epibranchial. Epibranchial 1 bears 0–3 long gill-rakers on outer margin and two or three short, cylindrical denticulate rakers along inner surface.

Pectoral girdle (Fig. 19)

Principal differences between pectoral girdle elements of *Macruronus* and *Merluccius* are in the *cleithrum*, which in the

former lacks the prominent dorsoposterior process of the latter (Inada, 1981:85; fig. 38); *coracoid*, which in *Macruronus* has a relatively short anteroventral process; and *postcleithrum*, which is longer and more deeply curved than in *Merluccius* with an arrow- as opposed to a club-shaped head (Inada, 1981; figs 39, 40).

Pelvic girdle (Fig. 20)

Noticeable differences occur in *pelvic bone* shape between *Macruronus* and *Merluccius*. In *Macruronus*, pelvic bone elongate with strongly developed lateral lamina; postpelvic process long and ventroposteriorly curved, articular surface for the fin rays short. In *Merluccius* pelvic bone broad with wide medial horizontal lamina and low lateral ridge; post-pelvic process long but straight, articular surface for fin rays extensive. *Macruronus* with 8 pelvic rays, *Merluccius* with 7.

Gosline (1963:12) noted that in *Microgadus* (Gadidae) the pelvic girdle has a medial projection which overlaps and ligamentously joins its partner, further remarking on the absence of 'such projections' in *Merluccius*. Rosen & Patterson (1969:432) take up Gosline's remark in referring to the pelvic bones of the fossil *Rhinocephalus* by stating that

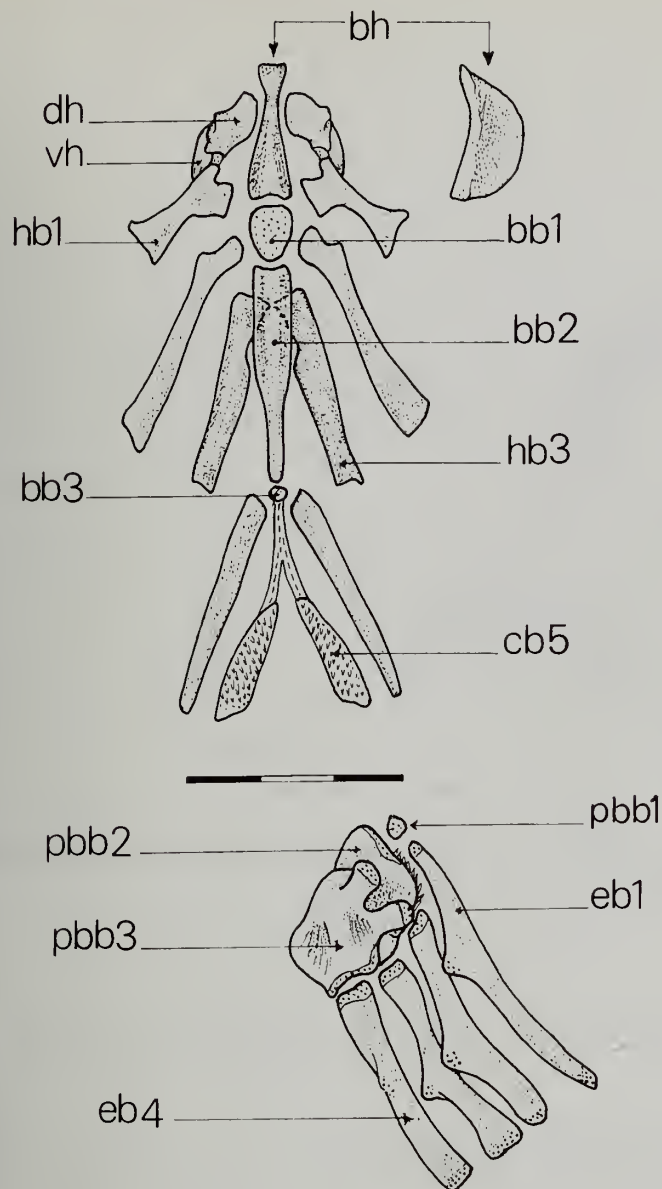


Fig. 17 *Macruronus magellanicus*, branchial arches. Above, lower elements in dorsal view; the basihyal is also shown in lateral view. Below, upper elements, right side, in dorsal view. Coarse stippling = cartilage. Alcian-alizarin stained preparation, (BMNH 1936.8.26: 342-51).

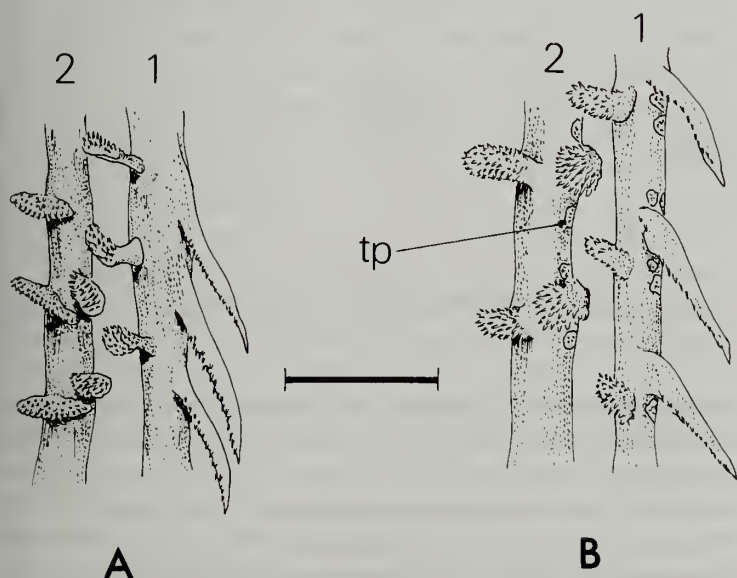


Fig. 18 Gill-rakers on the outer (1) and second (2) ceratobranchials of A, *Macruronus magellanicus* (BMNH 1936.8.26: 342-351); B, *Merluccius merluccius* (1971.7.21: 44-47; alcian-alizarin stained preparations).

this taxon resembles gadids and macrouroids and '... not that of merlucciids, in having medial processes'. Fahay (1989) in describing the pelvic girdle of *Steindachneria* takes this statement a stage further by remarking that the postpelvic processes are reduced and the pelvic bones meet *via* medial processes. He likens *Merluccius* and macrouroids where '... the posterior arms are directed posteriorly'. None of these statements is strictly correct, however. The so-called median processes of some gadids (*Gadus*, *Microgadus*, *Merlangius*) appear to be only an extension of the lamina anterior to the postpelvic process; the processes themselves still point posteriorly as is indicated by the pronounced ridges of bone which mark their position. Okamura (1970) considered the postpelvic process of several macrouroids to have been reorientated transversely.

Fahay's (1989) illustration of the pelvic girdle of *Steindachneria* shows that it differs little from that of *Bathygadus* (Howes & Crimmen, 1990, fig. 24), except that its postpelvic processes are angled somewhat anteriorly and as such I would interpret the pelvic girdle of *Steindachneria* as being plesiomorphic. On the other hand, the development of extensive laminae joining in the midline appears to be synapomorphic for the Gadidae, at least in those genera examined, *Gadus*, *Merlangius*, *Trisopterus*, *Melanogrammus*, *Theragra*, *Microgadus*.

Vertebral column (Fig. 21)

Macruronus magellanicus has 19-21 abdominal vertebrae (those, apart from the first four, bearing short, broad parapophyses) and 57-59 caudal vertebrae (those bearing a haemal spine; Fahay & Markle, 1984 give 58-60 for *M. novaezelandiae*); first four vertebrae are shorter than others, 2nd markedly compressed, only half the length of 5th. Prezygapophyses of 1st centrum ligamentously attached to compressed condyles of exoccipital; Baudelot's ligament attaches to lateral cavity of 1st centrum (see below). Third and 4th vertebrae each bear pair of ribs and epipleural ribs attach to tips of parapophyses of the other abdominal vertebrae.

Merluccius has 21-29 abdominal and 24-31 caudal vertebrae (Fahay & Markle, 1984). The abdominal elements bear extensive, wing-like parapophyses which become successively broader at the 11th or 12th vertebrae then diminish in size. Three or four pairs of ribs borne by 3rd-5th or 6th vertebrae (Inada, 1981:89).

Baudelot's ligament (Fig. 22) In *Macruronus* Baudelot's ligament thick, stretching from lateral cavity of 1st centrum, passing through head kidney and attaching laterally and complexly to pectoral girdle; the ligament shares an aponeurosis with postero- and anterolateral segments of epaxial muscle; it then divides into two broad bands one of which attaches to posteromedial rim of supracleithrum, the other to dorso-medial surface of cleithrum. In *Merluccius*, Baudelot's ligament is thin, running from 1st centrum; although divided and attached to both cleithral elements it does not join with any muscle segment.

Dorsal and anal fins. *Macruronus* has two dorsal fins. *First dorsal* comprises a minute first ray and 13 long, segmented rays all of which are supported by long, broad distal radials. *Second dorsal* confluent with caudal fin, has 90-92 rays supported by slim radials. *Anal fin* has 83 rays, the anterior six to eight produced, giving lunate border to anterior margin of fin.

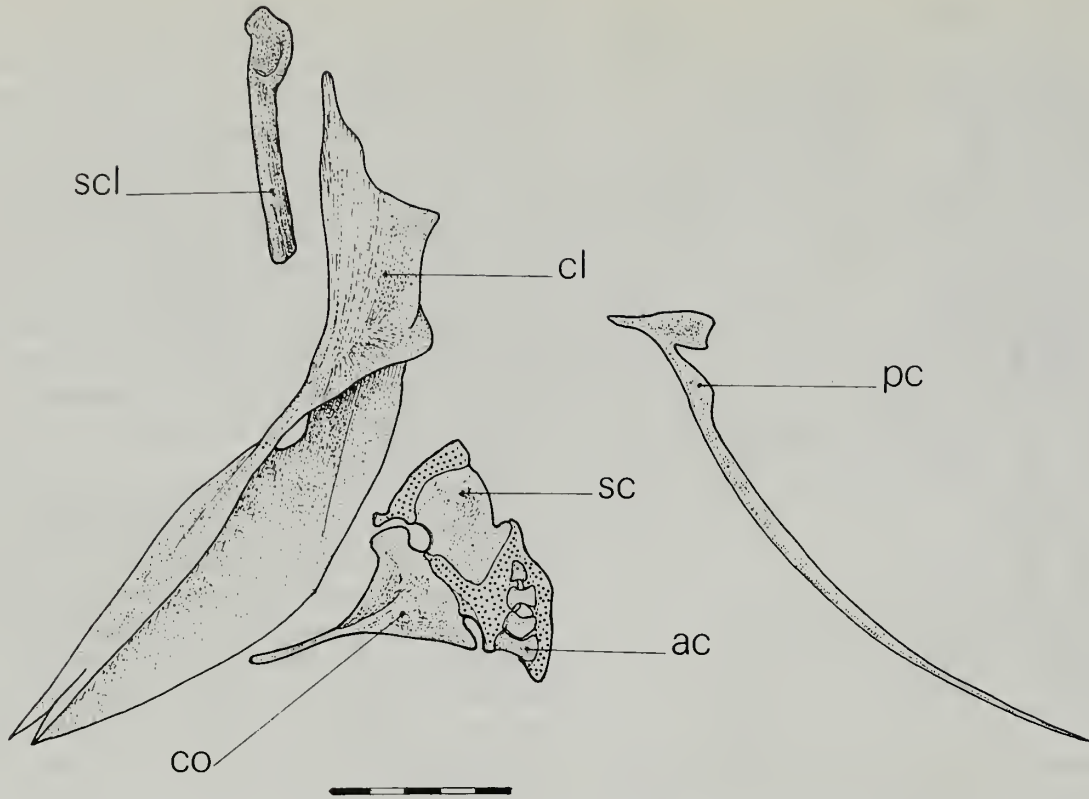


Fig. 19 *Macruronus magellanicus*, pectoral girdle in medial view. For clarity the coracoid, scapular and postcleithrum have been separated from the cleithrum (BMNH 1936.8.26: 342–351, alcian-alizarin stained preparation).

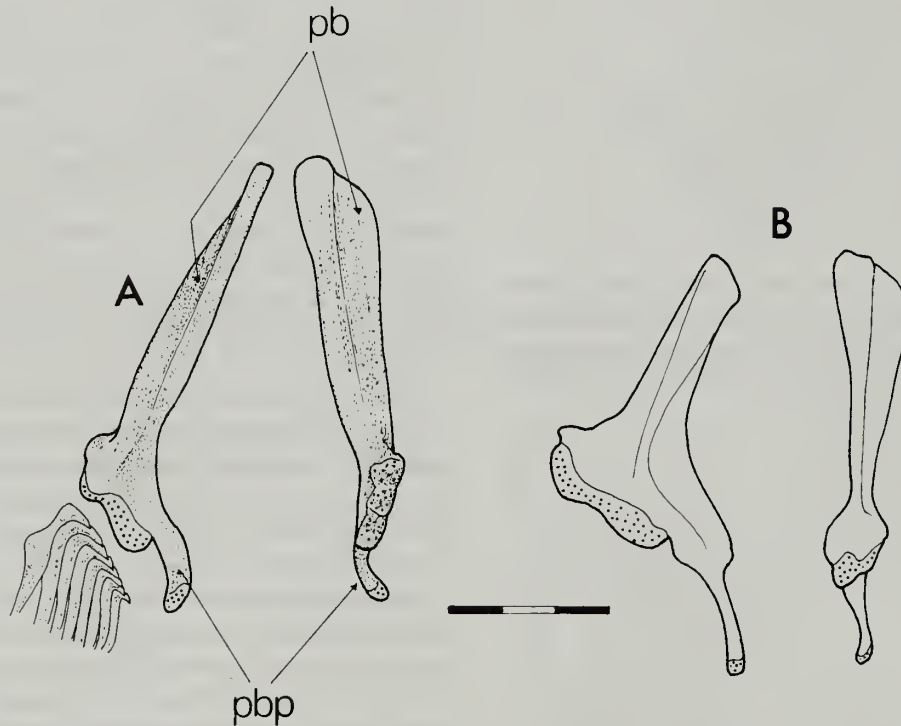


Fig. 20 Pelvic bone in dorsal (left) and lateral (right) views of; A, *Macruronus magellanicus* (BMNH 1935.8.26: 342–351) and B, *Merluccius merluccius* (1971.7.21: 44–49, alcian-alizarin stained preparations).

Merluccius has two dorsal fins. First dorsal 8–13 rays, second dorsal with 34–45; middle rays of second fin shorter than others, giving fin a notched appearance. Anal fin has 35–46 rays, also notched, anterior rays not produced. Dorsal and anal fins widely separated from caudal fin origin.

Principal differences in the vertebral column between *Macruronus* and *Merluccius* lie in the extreme development, in the latter, of the abdominal parapophyses which form a dorsal covering to the swimbladder, the lateral wall of which is firmly attached to the parapophyses. In *Macruronus*

the swimbladder is a cigar-shaped structure with an anterior bifurcation, and lacking intimate attachment to the parapophyses (Fig. 21).

In both genera the first radial of the first dorsal fin lies between 2nd and 3rd neural spines (Fig. 21). The neural spines and fin radials of *Macruronus* are thinner and larger than those of *Merluccius* and the dorsal laminae of the prezygapophyses taller. Although both genera have nearly equal numbers of abdominal vertebrae, *Macruronus* has more than twice as many caudal vertebrae, making a total

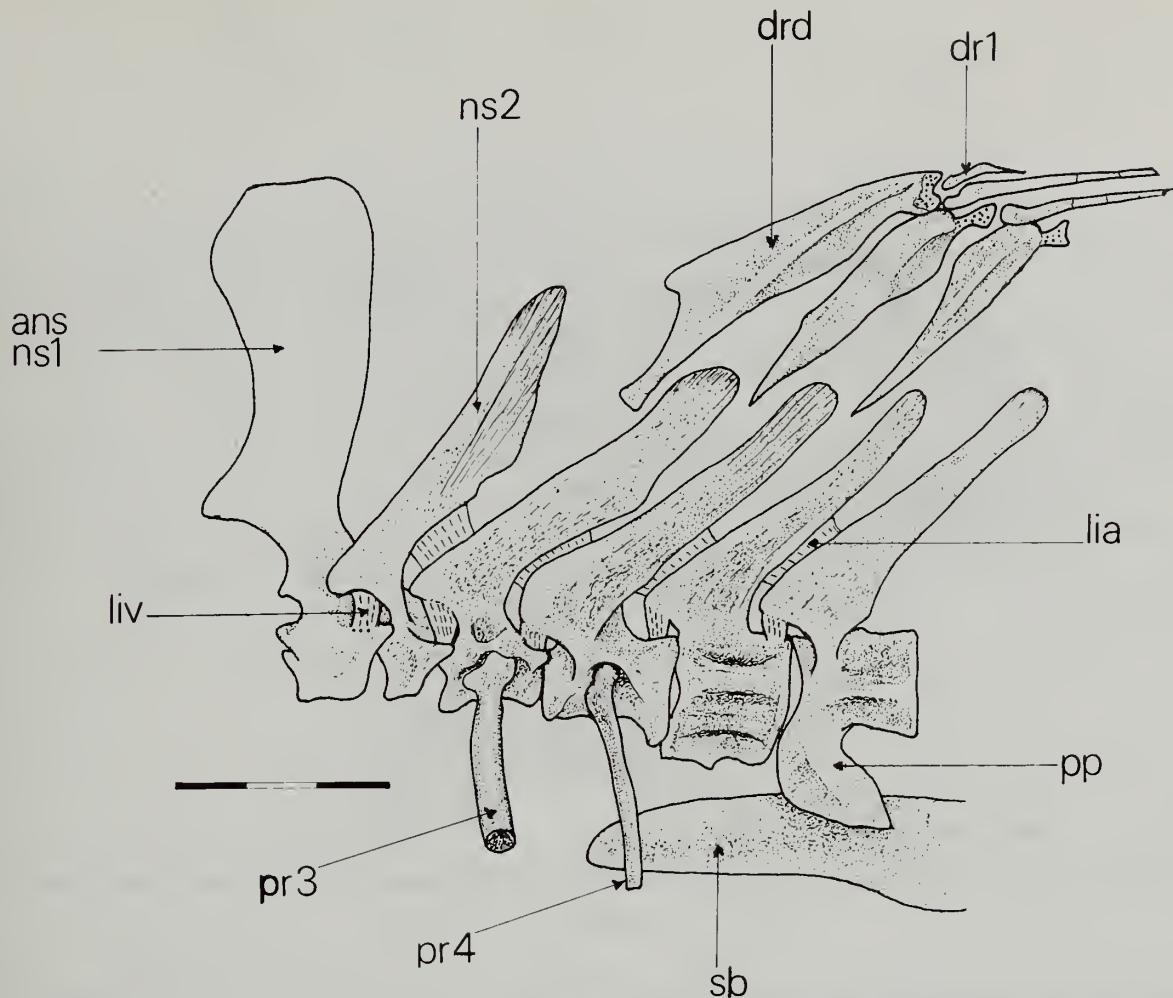


Fig. 21 *Macruronus magellanicus*, vertebral column and dorsal fin supports in lateral view. Drawn from dissection of BMNH 1936.8.26: 342–351, supplemented by radiographs.

difference of *ca* 20. There are nearly three times as many second dorsal fin rays and twice the number of anal rays in *Macruronus* than *Merluccius*.

Caudal fin skeleton (Fig. 23)

In *Macruronus* eight elements bear caudal fin rays *viz*, rays having a simple, rounded articulatory head as distinct from anvil or hammer shaped heads of dorsal and anal rays. Three vertebrae (terminal; two preural) are involved directly or indirectly with the caudal rays. Last centrum posteriorly compressed and upturned, having the appearance of a hypural plate to which attach four fin rays. Terminal centrum is assumed to be second ural centrum plus fused 3rd–5th hypurals, and possibly a uroneural. The penultimate vertebrae (assumed to be 1st preural plus 1st ural) is associated with four, posteriorly directed rod-like elements none of which is fused to the centrum. The two ventral elements have cartilaginous proximal and distal tips and each support fin rays. These appear to be the parhypural (anterior element) and fused 1st and 2nd hypurals (posterior element). Both bones articulate with deeply concave ventral surface of the centrum and lie adnate to one another and to the vertebral surface. The two dorsal elements have expanded proximal surfaces which interlock with one another and articulate with the dorsal surface of the centrum. The posterior of these two elements has broad lateral flanges; each element bears a caudal ray and are identified as epurals. The 2nd preural vertebra bears distinct neural and haemal spines, each of which appears to incorporate a radial. The

dorsal 'radial' lies adnate to the posterior surface of the neural spine leaving a small space between its proximal tip and the vertebral surface. The ventral element is basally co-ossified with the haemal spine but it does not extend to the base of the spine; the haemal arch is greatly reduced but is nonetheless present. Both dorsal and ventral 'radials' bear caudal rays. The 3rd preural centrum bears long, low-angled, neural and haemal spines each preceded by a long radial; the ventral radial bears what appears to be a caudal fin ray, but the dorsal radial articulates with a dorsal fin ray. Both dorsal and ventral radials bear anterior and posterior flanges, the anterior of which articulates with the head of the preceding radial.

The caudal fin skeleton of *Merluccius* is also symmetrical, the hypural plate supports 5 or 6 fin rays (Fig. 24). Combined 1st and 2nd hypurals articulate with 1st preural centrum and bear three fin rays. A parhypural lies between the lower hypural plate and the haemal spine of the 2nd preural vertebra and bears a single fin ray. Dorsally, two epurals, each bearing a fin ray, lie above 1st ural centrum; 2nd preural centrum bears compressed neural spine which supports single fin ray. Lying between the neural and haemal spines of 2nd and 3rd preural vertebrae are, respectively, X and Y bones, each bearing a fin ray.

Dorsal and ventral accessory bones, usually termed X and Y bones are lacking in *Macruronus*. Markle (1982) noted that X and Y bones can readily be distinguished from other autogenous elements because they have cartilaginous articulating surfaces. However, such a distinction only applies in small, incompletely ossified specimens; in adults of

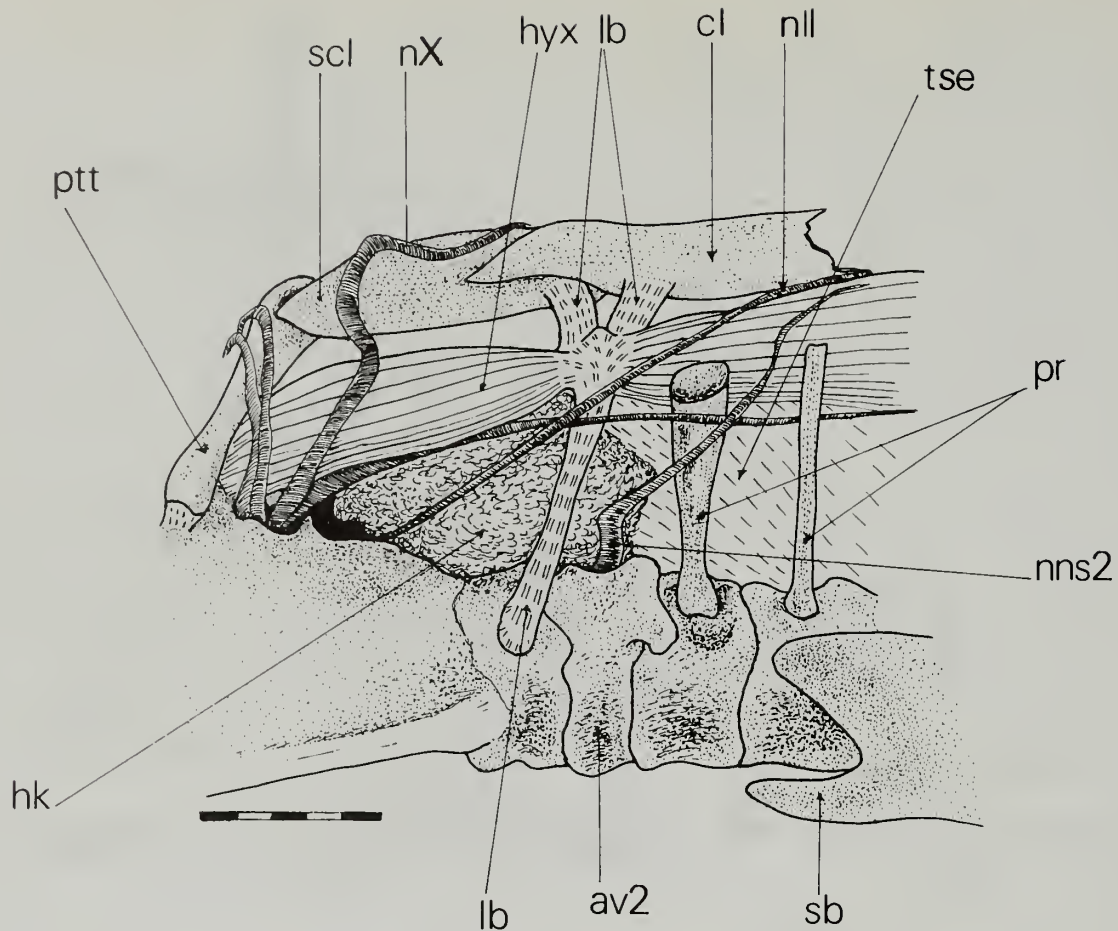


Fig. 22 *Macruronus magellanicus*, anterior part of the vertebral column and pectoral girdle in ventrolateral view showing the attachments of Baudelot's ligament (same specimen as in previous figure).

Merluccius X and Y bones are fully ossified. Besides, in partially ossified specimens the articulating surfaces of all autogenous elements are cartilaginous. The identity of X and Y bones is determined by their position, which is always between the second and third preural neural and haemal spines.

Like Markle (1982) I find 'extra' or bifurcate neural and/or haemal spines on PU2 (Markle's PU1). I have found in *Merluccius* the development of extra neural and haemal spines on the second preural vertebra. In one specimen (Fig. 25A) the posterior neural spine appears to be a composite element, viz the spine plus a co-ossified radial; thus resembling the situation in *Macruronus* (see above). In a second specimen (Fig. 25B) a single, short, spine-like process extends from the base of the neural spine to stand between the spine and the X bone. In a specimen of *Gadus morhua* (Fig. 26) the neural and haemal spines of the second preural vertebrae are clearly composite elements. The halves of the neural and haemal spines grip lamellate elements (probably the X and Y bones), that associated with the haemal spine being contiguous with the parhypural.

Fahay & Markle (1984) have suggested that the acquisition of X and Y bones and modifications of the posterior preural neural and haemal spines were necessary precursors of the gadoid symmetrical tail fin.

Caudal fin muscles (Fig. 27)

In *Macruronus* there are two thin and narrow superficial layers of longitudinal muscles running dorsally and ventrally along the posterior part of the vertebral column. These

muscle bands are continuous anteriorly with the epaxial and hypaxial musculature; they insert *via* thin tendons respectively to the upper (third) and lower (fifth) 'caudal' rays. Since these muscle bands have no attachments to the neural and haemal spines or to the lateral surfaces of the centra, other than by loose connective tissue, I regard them, as respectively, epaxial and hypaxial muscles. Their insertion to the caudal rays is not unlike that of the epaxial and hypaxial muscles in other teleosts (eg. *Elops*, shown in Winterbottom, 1974, fig. 48). If the insertions of the hypaxial and epaxial muscle bands should be the criteria defining a caudal ray, then the number of rays would be 7 rather than 11 as given above (cf. Figs 23 & 27A). The deeper dorsal muscle layer runs posterodorsally from the supporting radials to insert on the bases of the upper caudal rays. There are two components of these muscles, one running to the shaft of the ray, the other passing mesad to the base of the ray. The fibres originating from the terminal centrum are clearly differentiated into a separate segment (hsh, Fig. 27A). Those anteriorly, however, become continuous with and indistinguishable from, the *erectores* and *depressores dorsales* of the dorsal fin rays. The deeper ventral muscle layer is similarly arranged to the dorsal, except that there is no terminally differentiated bundle; the series running from the ventro lateral cavities of the centra and the supporting radials to insert on the ventral caudal rays. Long, narrow bundles of fibres ('*interradialis*') connect the caudal rays with one another. The central caudal fin ray is identified as such by the angle of the '*interradialis*' fibres connecting it with the immediate upper and lower rays, viz posterodorsally or posteroventrally (Fig. 27A).

The caudal fin musculature of *Merluccius* is essentially

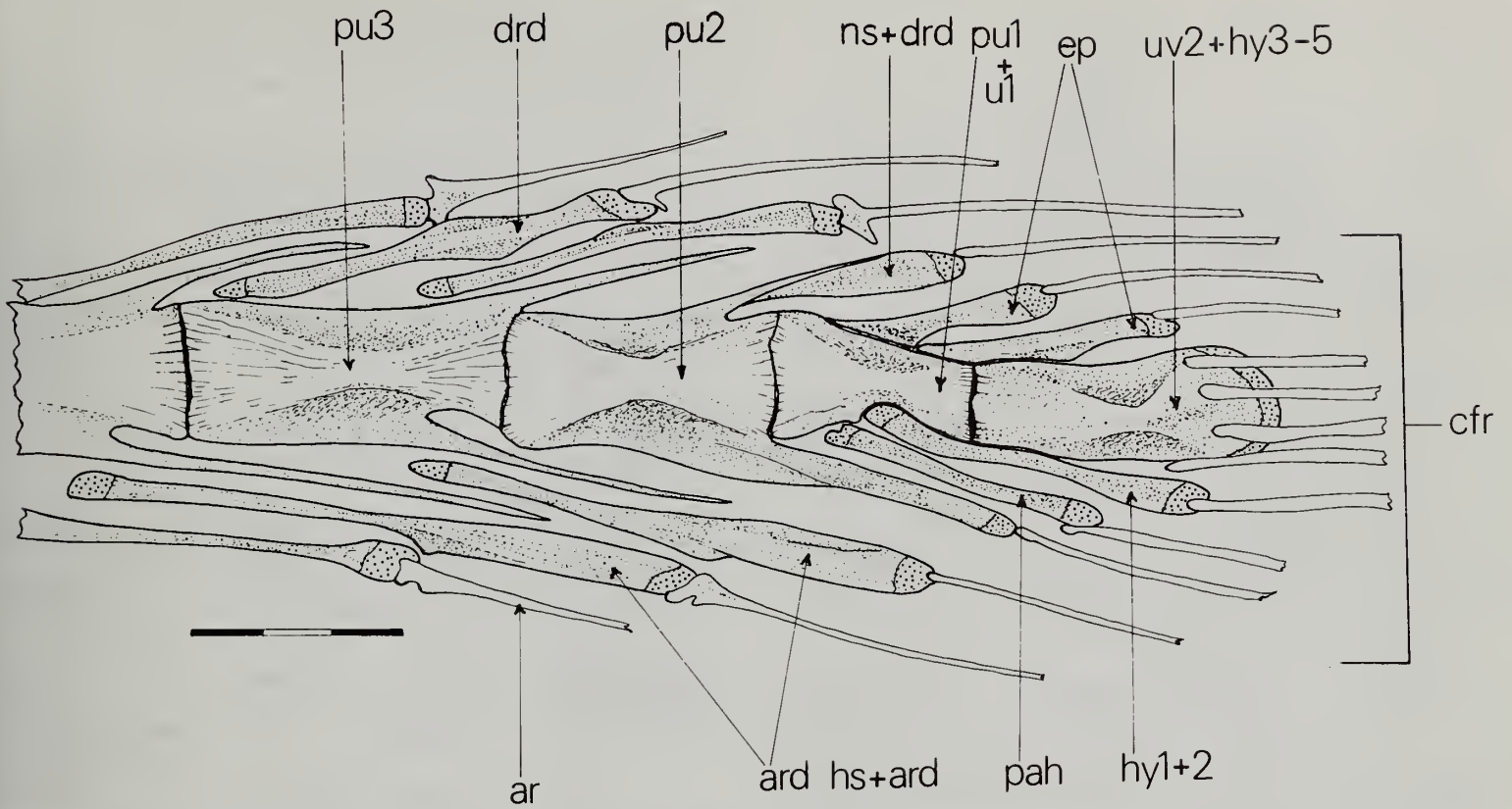


Fig. 23 *Macruronus magellanicus*, caudal fin skeleton (BMNH 1936.8.26: 358-63, alcian-alizarin stained preparation of tail region).

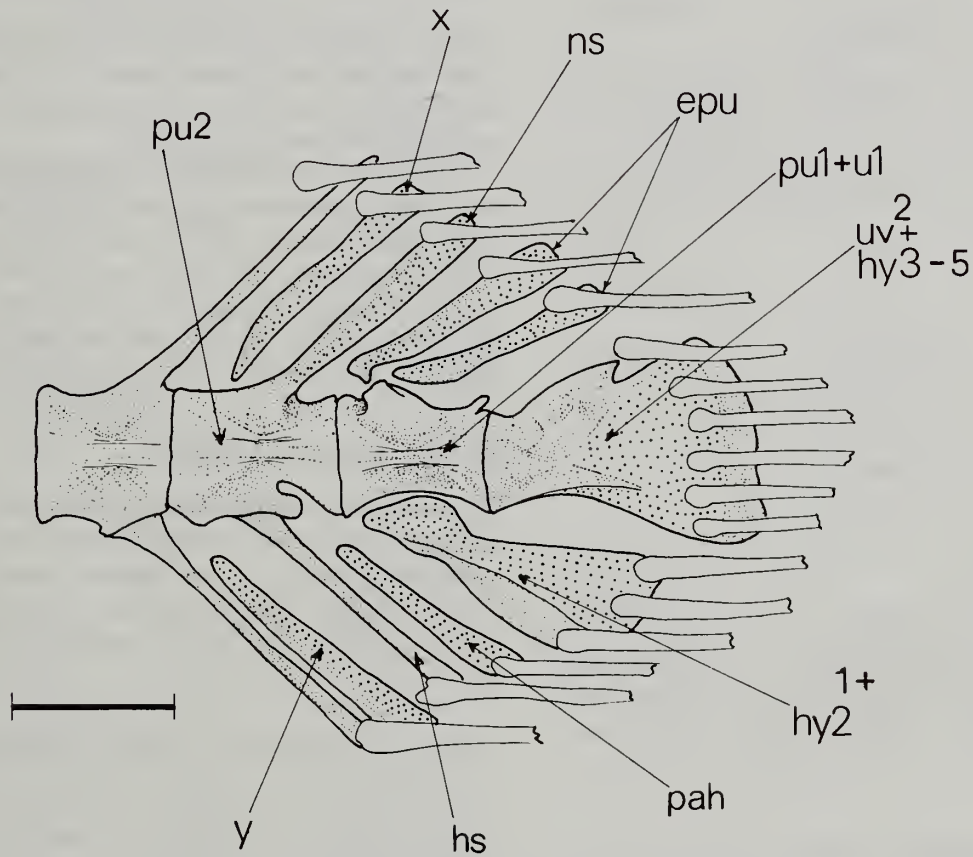


Fig. 24 *Merluccius merluccius*, caudal fin skeleton (BMNH 1976. 8.30: 87-96, alcian-alizarin stained preparation).

similar to that of *Macruronus*, as indeed it is in other gadoids examined. In *Gadus* the two component muscle insertions to the base of the caudal rays is clearly marked and appears no different from the arrangement of *depressores* and *erectores* muscle of the dorsal and anal fin rays. *Muraenolepis* exhibits a

simplified system of caudal fin musculature in that no separate terminal segment arising from the hypural plate is differentiated. '*Interradialis*' muscles interconnect the posterior 22nd dorsal and 'caudal' rays and the posterior 18 anal rays (dorsal and anal ray numbers counted forward from the median caudal ray).

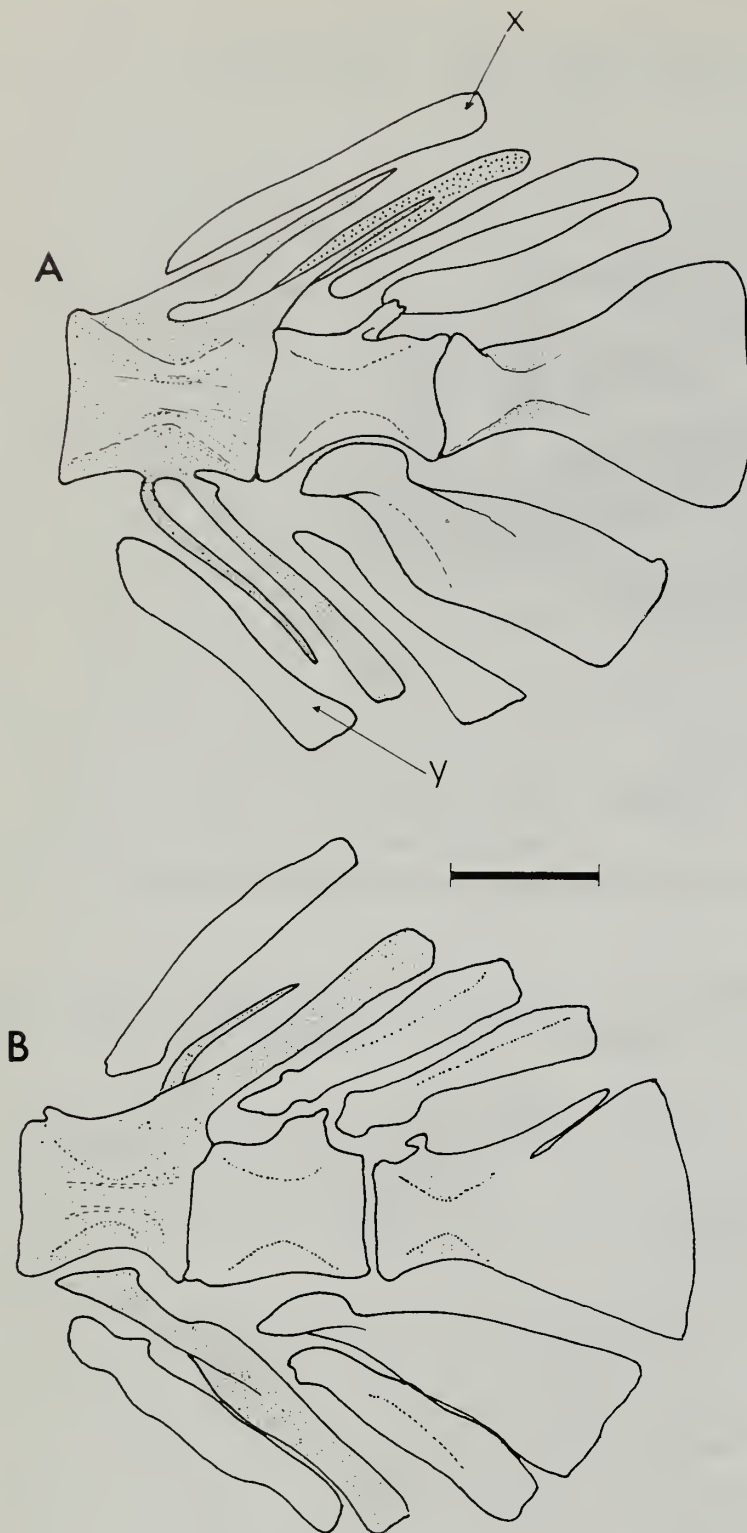


Fig. 25 Caudal fin skeletons of *Merluccius merluccius* in lateral views. Two specimens (ex. BMNH 1971.7.21: 44–59) showing individual differences (see text). Second preural vertebra and associated elements are shaded; cartilage is indicated by coarse stippling. Scale=1.0mm.

Epaxial muscle insertion (Fig. 26A)

In *Macruronus* epaxial musculature extends well forward to insert on the cranium above the posterior region of the orbit. Central section of the muscle bloc inserts along supraoccipital crest, its fibres forming an angle of 20° to it. Anterolaterally a separate muscle segment branches from main body, continues forward and inserts on the diagonal frontal ridge posterior and medial to orbit. Epaxial muscle covers dorsal posttemporal limb.

In *Merluccius epaxialis* inserts mostly along posterior

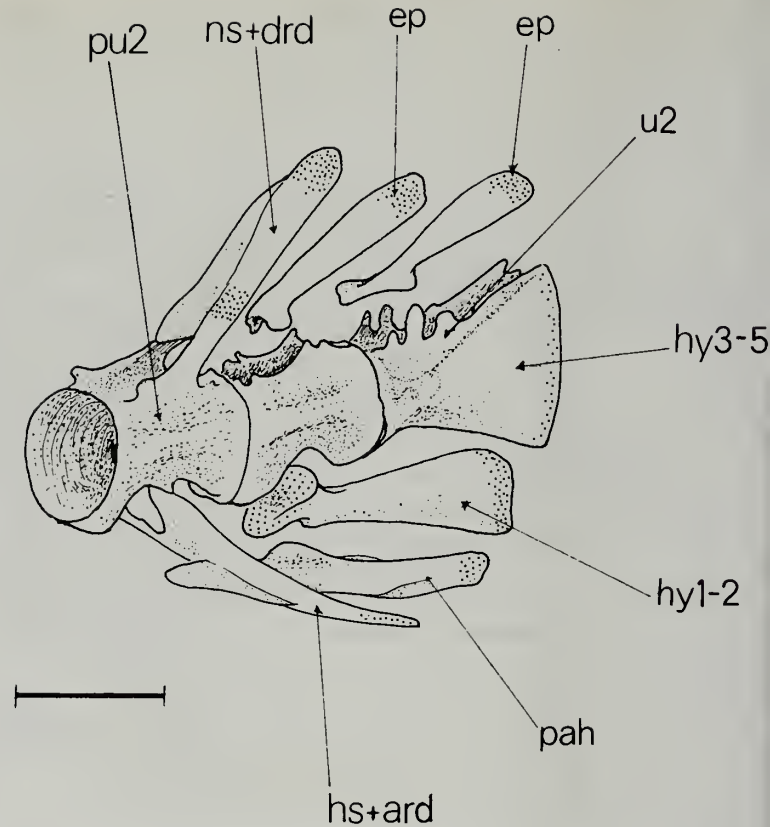


Fig. 26 Caudal fin skeleton of *Gadus morhua*, lateral aspect, viewed anterodorsally (ex. BMNH 1971.2.16: 628–33). Scale=0.5mm.

border of dorsal posttemporal limb; medially it inserts on supraoccipital and frontal crests. A small ventrolateral segment passes forward beneath posttemporal limb to insert in posttemporal fossa (Fig. 26B).

The *Merluccius* condition appears the more derived of the two. Among other gadoids it is usual for the *epaxialis* to insert along the posterior slope of the cranium; the medial fibres attach to the supraoccipital crest. In all other taxa examined the posttemporal limb is covered and the *ramus lateralis accessorius* (RLA) nerve passes lateral to the epaxial segment (Fig. 26C,E); RLA is absent in *Macruronus* and *Merluccius*.

Rectus communis muscle

Macruronus is unique in that the *rectus communis* muscle attaches, posteriorly, to the 5th ceratobranchial rather than, as in other gadoids, to 4th (Howes, 1988a:46). Anteriorly, the muscle attaches aponeurotically to the *sternohyoideus* as in the majority of other gadoid families (Howes, 1988a, table 2: 46).

Ramus lateralis accessorius (RLA) nerve

In most gadoids the recurrent branch of the facial nerve, RLA, leaves the cranium *via* a foramen in the parietal or between parietal and epioccipital. This foramen is absent in both *Macruronus* and *Merluccius*. Svetovidov (1948: 14) claimed that in *Merluccius* the foramen is covered by bony crests, but further (p. 133) remarks that parietal crests above the foramen are not developed; both statements are incorrect. Freihofer (1970) noted RLA as apparently absent in *Merluccius*. My observations confirm this absence.

Freihofer (1970) noted in *Merluccius* presence of accessory segmental lateral-line nerves serving the base of the pectoral fin. These also occur in *Macruronus*. Similar nerve patterns

are reported by Freihofner (1970) to occur in a variety of paracanthopterygian, acanthopterygian and lower euteleostean taxa. This distribution suggests either a plesiomorphic or homoplastic presence (see discussion, p. 99)

Table 1. Comparison between *Macruronus*, *Merluccius* and other gadoids of characters discussed or noted in the text

Character	<i>Macruronus</i>	<i>Merluccius</i>	Other gadoids
Lateral ethmoid wing	flat	cone-shaped	cone-shaped in Gadidae, flat in others
Mesethmoid	gently sloped	acutely sloped	vertical in most, sloped in Melanonidae and Bathygadidae
Vomer	toothed	toothed	toothed; edentulous in Eulichthyidae and Bathygadidae
Nasal	narrow, trough-like	trough-like	various, broad in Bathygadidae
Cranial depth	deep	shallow	various, often shallow
Frontals	separate	separate	separate in most but fused in Gadidae and some Phycidae
Medial frontal crests	thick, enclosing central medial cavity	thin, no medial cavity	thin, variously developed or absent, enclosing anterior cavity in Gadidae
Frontal sensory canal	covered by broad roof	roof lacking	roof lacking
Frontal ventral lamina	converge	parallel	parallel (enclosed canal in Moridae)
Sphenotic border	indented	straight	straight
Prootic with medial projection	formed as a transverse wall	shelf-like	only in Gadidae
'Posterior myodome'	absent	present	absent
Parasphenoid	thin, round in cross-section	thick, flat in cross-section	variously developed usually thick and flat
Intercalar	forms posterior margin of lateral cranial wing	forms only part of posterior margin	forms posterior margin only in <i>Phycis</i> and <i>Muraenolepis</i>
Supraoccipital crest	low, embraced by 1st neural spine	high, embraced by 1st neural spine	variously developed usually only partly embraced by 1st neural spine
Exoccipital condyles	acutely sloped	gently sloped	usually horizontal
Posttemporal	covered by epaxial muscle, ventral limb long, in contact with posterior border of	exposed, ventral limb widely separated from intercalar, lies in same	covered by epaxial muscle, ventral limb separated from intercalar and pterotic margin, dorsal and

Extrascapulars	intercalar; dorsal and ventral limbs not in same vertical plane	vertical plane as dorsal limb	ventral limbs not in same vertical plane
Palatine contacts	mesethmoidal part of lat. ethmoid	4, lateral and medial mesethmoidal part of lat. ethmoid	3 or 4, lateral and medial mesethmoidal part of lat. ethmoid, except in Melanonidae, Bathygadidae and Steindachneriidae
Palatine origin of muscle A1B β Retroarticular	ventral cavity	lateral cavity	none
Labial ligament attaches	anteriorly extended	short, triangular	short, triangular or L-shaped usually centre but anteriorly in Bathygadidae and Melanonidae
Ento-and meta-pterygoid	in contact	widely separated	in contact
Hyomandibula flange	absent	with two ventrally directed processes	with a single ventrally directed process (only in 'higher' gadoids)
Suboperculum	broadly triangular	oblong	various, usually broadly triangular
Interopercular-posterohyal joint	absent	present	present only in 'higher' gadoids
Interopercular posterior border	straight	rounded	rounded
Basihyal	elongate	short	short
1st pharyngobranchial	absent	absent	reduced
Infraorbitals	5th with canal enclosed; 1st contacts ventral margin of lateral ethmoid	5th open; 1st contacts lateral margin of lateral ethmoid	5th open; 1st contact is variable, usually ventro-posterior surface of lateral ethmoid present
Cleithrum with dorsoposterior process	absent	present	
Vertebrae	Abdominal Caudal 58-60	21-29 24-31	12-13 80+
Parapophyses	Slightly developed	Extensively developed	Variable but never as in <i>Merluccius</i>

MERLUCCIID CHARACTERS

From the foregoing comparisons it is clear that *Macruronus* differs from *Merluccius* in several features (summarised in Table I); most are autapomorphic and in this respect *Macruronus* is no less widely divergent from *Merluccius* than from any other gadoid. There are, however, seven shared characters between the two genera which at face value appear to be synapomorphic, viz:

1. V-shaped frontal crest; 2. fusion of supraoccipital crest with 1st neural spine; 3. palatine origin of muscle A1b; 4. prootic transverse septum; 5. absence of RLA nerve; 6. reduced first pharyngobranchial; 7. high number of abdominal vertebrae.

1. V-shaped frontal crests

According to Regan (1903) both *Macruronus* and *Merluccius* possess frontals bearing an anteriorly divergent ridge or crest. This V-shaped frontal crest pattern has been considered as a character for the Merlucciidae. However, the conditions in *Macruronus* and *Merluccius* are quite different. In *Macruronus* the medial frontal crest encloses a narrow, posterior central cavity. The crest also forms the medial wall of the cavity housing the frontal sensory canal which opens anteriorly through a wide aperture (Fig. 2).

In *Merluccius* the frontal ridges are widely divergent and do not enclose a narrow central cavity but a broad, open area lacking a medial longitudinal septum and transverse foramina; frontal sensory canals lack any bony covering (Fig. 5).

Markle (1989) considered a V-shaped pattern of frontal crests to be derived and one characterising the Merlucciidae. His argument for the specialized nature of this pattern is not convincing, however, since it is based on a comparison with a similar morphology in the unrelated *Opsanus*, which Gregory (1933) thought was a consequence of forces generated by *adductor mandibulae* muscles. This is a completely unfounded functional hypothesis. In fact, the pattern of frontal ridges of *Merluccius* is not unlike that of *Bathygadus* (see Howes & Crimmen, 1990); in both the crests appear to be merely the medial walls of the frontal canals left through the attrition of a roof. This is a common attribute among gadoids and macrouroids and the V-shape pattern appears to be plesiomorphic.

2. Fusion of supraoccipital crest with the 1st neural spine.

As observed by Fahay (1989) in macrouroids the neural spine is ligamentously attached to the supraoccipital which is also the case in the plesiomorphic gadoid family Bathygadidae. In other gadoids there is some variability; for example in the Moridae, Ranicipitidae and most Phycidae only the tip of the supraoccipital process is embraced by the lamina of the neural spine. In Lotidae, *Lota* and *Brosme* have the supraoccipital crest firmly united with the spine, whereas in *Molva* the crest is embraced by the spine, as it is in the phycid *Gaidropsarus*.

As described above, in *Macruronus* and *Merluccius* lamina of the 1st neural spine is anteriorly extended so as to embrace almost the entire posterior area of the supraoccipital crest. Fahay's (1989) reason for interpreting the similar situation in *Steindachneria* as derived is ontogenetic fusion between neural spine and supraoccipital crest. If a similar ontogenetic situation occurs in *Macruronus* and *Merluccius* this would add support to Fahay's interpretation of its derived nature.

Although referred to here as the 1st neural arch and spine, the structure of this element and its articulation with the exoccipital and basioccipital in *Macruronus* suggests that there is more than a single element involved. The pattern of occipital-vertebral contact in 'paracanthopterygians' is confusing. According to Rosen (1985) a synapomorphy for gadiforms and some ophidiforms is the anterior position of the exoccipital facets with respect to the articular surface of the basioccipital, and the corresponding forward extension

of the first neural prezygapophyses. In *Macruronus* the exoccipital facets lie in the same vertical plane as the basioccipital facet and the prezygapophyses are not anteriorly extended, nor do they abut the exoccipital facets but are joined to them ligamentously (Fig. 29A). The basal anterior extension of the neural arch, likewise does not form a firm union with the sloped dorsoposterior surface of the exoccipital articular extensions, but is ligamentously attached in the same way as each vertebral neural prezygapophysis is attached to the preceding centrum. Grounds for believing that two arches are involved in the first neural element are the presence of a prominent vertical ridge down the posterior part of the neural spine and a correlated change in the direction of the bony striae from anterodorsal to posterodorsal; furthermore, two hollow shafts are present within the neural spine (Fig. 29B). I suspect that the first neural spine has become dissociated from its centrum which itself has become separately incorporated into the basioccipital (Fig. 29A). Similarly, in *Merluccius* there is no proper exoccipital facet, the terminal points of the bone being hollow and joined ligamentously to the neural arch (Figs 5A; 8). Incorporation of a first centrum within the basioccipital was suggested by Faruqi (1935) from an ontogenetic study of *Melanogrammus*.

3. Palatine origin of muscle A1b

Howes (1988) noted that in *Macruronus*, *Lyconus* and *Merluccius* the anterior section of *adductor mandibulae* muscle A1b originates from the lateral face of the palatine. However, in *Macruronus* and *Lyconus* the muscle originates from a deep ventral cavity confluent with a similarly deep ectopterygoid channel (p. 85). Only in *Merluccius* does the muscle originate from a lateral fossa.

Other differences between the three genera were noted by Howes (1988); pinnate nature of muscle A1a and the more anterior origin of A1b in *Macruronus* and *Lyconus*, having the correlated effect of displacing the ramus mandibularis of the trigeminal nerve past the posterior point of the muscle rather than running across it as in *Merluccius*. In all three taxa muscle A1b occupies a medial plane as A1a, as in more plesiomorphic gadoids (eg Bathygadidae, Moridae). Like those taxa, however, *levator arcus palatini* is extensive covering the upper part of *adductor mandibulae* A1. In outer adductor muscle morphology both *Macruronus* and *Lyconus* differ appreciably from *Merluccius* (Howes, 1988).

4. Prootics with transverse septum

In both *Macruronus* and *Merluccius* each prootic bears a medial process which sutures with its partner in the midline forming a transverse septum (p. 83).

Merluccius has a ventromedial perforation in the septum from which the recti muscles originate. In this sense the prootic cavity acts as a posterior myodome. In *Macruronus* the recti originate from the medial surfaces of the ascending processes of the parasphenoid, which is also the condition in other gadoids. Only in Gadidae is there a similar prootic extension (Fig. 6D) but in this taxon the processes remain separated from one another in the midline and form broad shelves. As in other gadoids the recti muscles originate anteriorly to the shelf, entirely within the boundary of the parasphenoid. The septal walls in *Macruronus* are medially thickened and posteriorly convex, and stem from the anterior border of the prootic. In contrast, those of *Merluccius* are of equal thickness, horizontal, posteriorly concave and extend from the prootic walls.

In Moridae there occurs a unique condition where, rather than the prootics meeting across the midline, the ascending processes of the parasphenoid are reorientated transversely and are sutured in the midline forming a septum comparable to that formed by the prootics in *Macruronus* and *Merluccius* (Fig. 6C). The recti muscles originate from the anterior facing surfaces of the parasphenoid processes.

Absence of a posterior myodome in gadiform fishes is considered derived (see Patterson, 1975), a feature most probably due to the modification of the anterior part of the prootic in forming the common optic-trigeminal foramen. In *Merluccius* development of a posterior myodome with medial extensions of the prootic forming its roof is undoubtedly a secondarily derived state. In this respect *Merluccius* differs from both *Macruronus* and Gadidae, in which taxa the recti muscles originate anteriorly to the prootic cavity. Despite this difference, prootic morphology of *Merluccius* has greater similarity to that of Gadidae than to *Macruronus*. In the two former taxa the medial extension is horizontal, emanating from the prootic side-wall whereas in *Macruronus* it is vertical, extending from the anterior wall. The condition in *Merluccius* is considered derived from the gadid, whereas that of *Macruronus* has been independently evolved.

5. Absence of the ramus lateralis accessorius (RLA) nerve.

Too few taxa have been surveyed for this character to say with assurance that absence of RLA is unique to *Macruronus* and *Merluccius*. In other gadoids presence of a foramen in the cranial roof for the dorsal branch of the RLA is an indication of its dorsal ramification.

Macruronus and *Merluccius* have flat crania and both have more complex, but different, insertion of the epaxial musculature than other gadoids. *Merluccius* has an exposed posttemporal whereas in *Macruronus* it is covered by muscle fibres. Loss of RLA is possibly correlated with absence in both taxa of mucoserous pores (genipores of Svetovidov, 1948) since the dorsal branch of RLA is responsible for innervating epidermal cells. Furthermore, the lateral line in both genera is more elevated along the body than in other gadoids.

Further investigation of RLA pathways is required to determine whether these factors are correlated. On face value absence of RLA might be considered synapomorphic loss for *Macruronus* and *Merluccius*, but in the light of distribution of other, positive, synapomorphies, this negative one is regarded as homoplastic.

6. Reduced 1st pharyngobranchial.

Markle (1989) noted the reduction and lack of ossification of pharyngobranchial 1 in gadoids other than the Melanonidae, Moridae and Steindachneridae. Pharyngobranchial 1 is reduced and cartilaginous in Bathygadidae, considered a plesiomorphic gadiform lineage (Howes, 1988; Howes & Crimmen, 1990). Widespread reduction of this element throughout gadoids cannot therefore justify its use as a synapomorphy linking *Macruronus* and *Merluccius*.

7. Numerous abdominal vertebrae.

Markle (1989) considered a high number of abdominal vertebrae (20 or more) to be synapomorphic for a group of gadoids comprising the Gadidae, Lotidae and Merlucciidae. *Macruronus* has 19–21, *Merluccius* 21–29 and in this respect is

the more derived taxon. In fact, *Macruronus* has fewer abdominal vertebrae than the lotids *Lota* and *Molva* (respectively with 23–26; 25–36), the gadids *Eleginus* (21–24), *Gadus* (18–22), *Merlangius* (20), *Microgadus* (17–22), *Micromesistius* (24–26), *Pollachius* (20–23) and the muraenolepid, *Muraenolepis* 20–21 (data from Fahay & Markle, 1984).

Macruronus has 58–60, caudal vertebrae which far exceeds the number in *Merluccius* (24–31), but is exceeded by the other merlucciid, *Lyconus* (72 in the only available specimen, with broken-off tail). In other 'tail-less' gadoids, bathygadids have 70+; *Steindachneria*, ca 80.

In view of its widespread distribution, a high number of abdominal vertebrae cannot be taken as synapomorphic for *Macruronus* and *Merluccius*. Similarly, numerous caudal vertebrae in both gadoid and macrouroid taxa suggest a plesiomorphic condition. It follows, therefore, that taxa with reduced numbers of caudal vertebrae are the more derived. It may even be that the symmetrical caudal skeleton of more derived gadoids is a feature acquired in conjunction with reduction of a tapered tail (p. 106).

In summary, none of the seven characters listed above as possible synapomorphies between *Macruronus* and *Merluccius* can, under detailed scrutiny, be upheld. Indeed, *Macruronus* also lacks those characters which I consider to delimit the subgroup of gadoids which contains *Merluccius*. These synapomorphies are:

1. Posterohyal-interopercular joint.
2. Cone-shaped lateral ethmoid
3. Hyomandibular with lateral shelf

1. Posterohyal-interopercular joint.

Lauder & Liem (1983: 150) pointed out that 'Gadids and merlucciids (*sic*) share an epihyal-interopercular joint' which they described as a medially directed process stemming from the interopercular and articulating with the posteroventral corner of the posterohyal (epihyal). Howes (1989) and Markle (1989) have also referred to this feature as a synapomorphy uniting a subgroup of gadoids; Gadidae, Lotidae, Ranicipitidae, Muraenolepididae, Phycidae, Bregmacerotidae and Merlucciidae. Both authors treated *Macruronus* as a merlucciid and as possessing this synapomorphy, but in fact, the taxon lacks this feature. Although the interopercular bears a depressed, cartilaginous articular surface, there is no strongly developed osseous process which forms an interopercular socket (p. 88).

2. Cone-shaped lateral ethmoid.

In comparing the Eocene gadoid *Rhinocephalus* to *Merluccius*, Rosen & Patterson (1969) remark on the shared character of a cone-shaped, posteriorly open, lateral ethmoid also being present in gadids.

Merluccius, displays the characteristic cone-shape only poorly since the lateral ethmoid wing is thickened, directed outward and has a broad curvature (Fig. 30A). I agree, however, that a characteristic cone-shaped morphology of the lateral ethmoid is a feature common to certain gadoids. It is present in all genera of Gadidae examined, *viz* *Gadus*, *Pollachius*, *Theragra*, *Merlangius*, *Melanogrammus*, *Trisopterus* (Fig. 30C). Among the Lotidae it is clearly evident in *Molva*, *Brosme* and *Lota*, despite the lateral ethmoid flaring outward. Among Phycidae, *Gaidropsarus* and *Ciliata* (Figs 30B & D), although both having a laterally directed ethmoid wing nonetheless preserve the cone-like

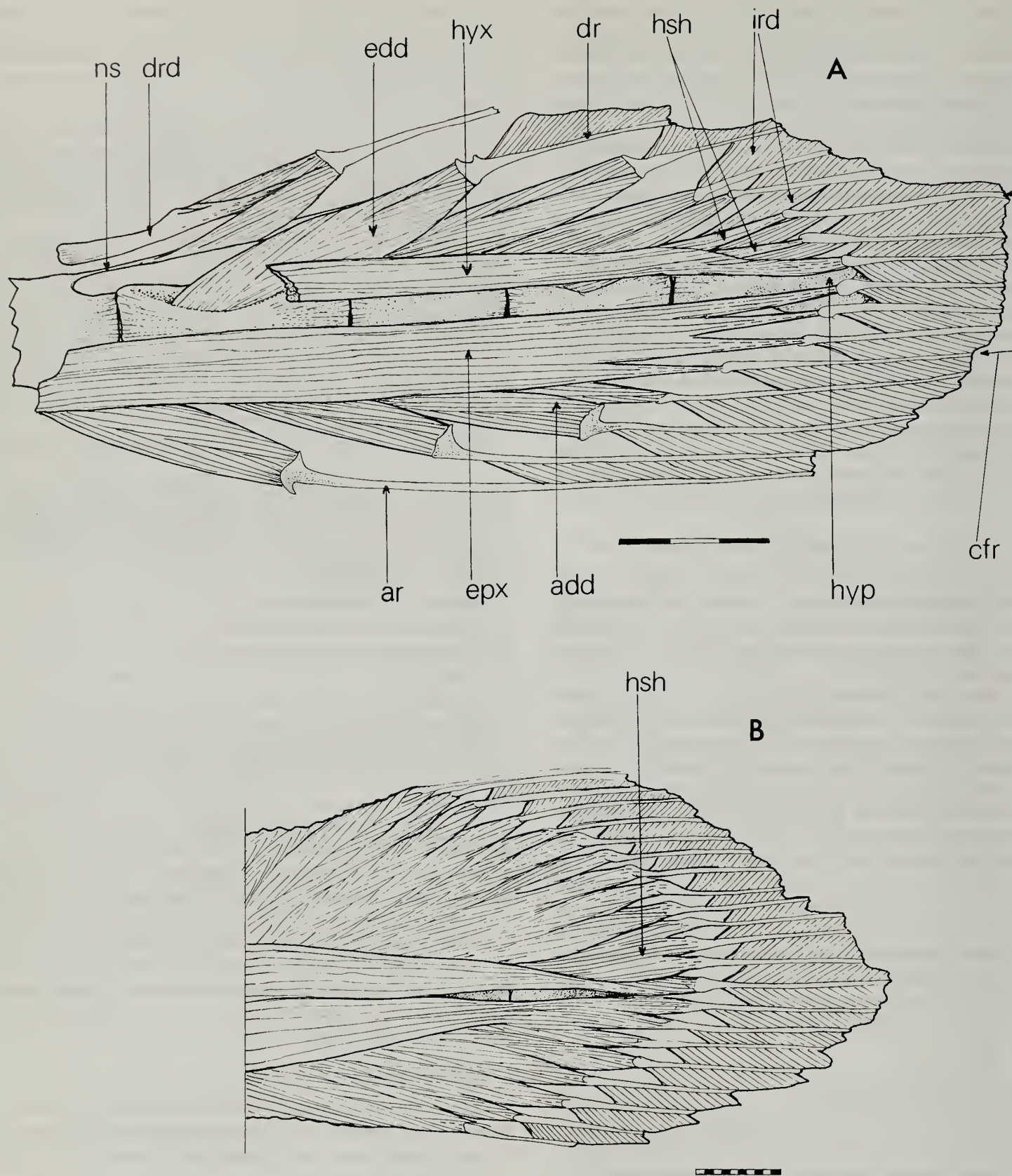


Fig. 27 Caudal fin muscles in lateral views of; A, *Macruronus magellanicus* (superficial musculature removed; BMNH 1936.8.26: 358–36) and *Merluccius capensis* (1935.5.2: 118–119).

shape, which in *Ciliata* is virtually tubular. In *Phycis*, however, the lateral ethmoid wing is a broad, downwardly curved lamina showing no trace of modification. In the Ranicipitidae, the lamina is thin and directed outwards in a near-horizontal plane (Fig. 30E), while that of Muraenolepididae is narrow, thick and downwardly directed (Howes, 1987; fig. 4b). In both latter families the lateral ethmoid appears much modified and does not exhibit any evidence of a gadid

morphotype. In other gadoid families the lateral ethmoid wing has, what is considered to be the plesiomorphic form namely, a broad, downwardly directed lamina (typically in Bathygadidae, Howes & Crimmen, 1990; fig. 2B).

As far as *Macruronus* is concerned, the lateral ethmoid bears no resemblance to the gadid-type, nor to the plesiomorphic form, rather it is intermediate. Unlike *Merluccius*, however, which bears traces of a cone-shaped, gadid-type

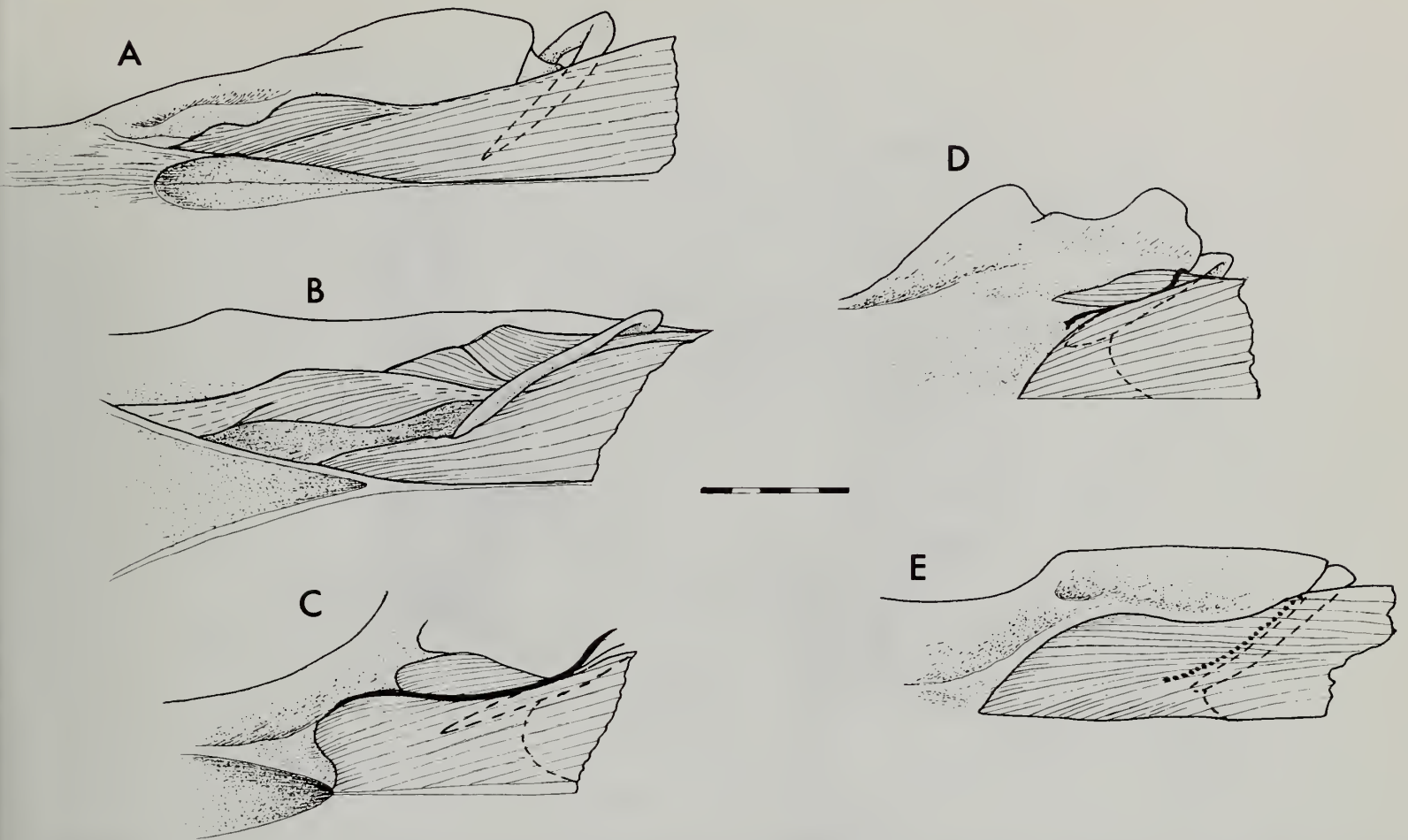


Fig. 28 Epaxial muscle insertion (dorsal aspect) of; A, *Macruronus magellanicus* (BMNH 1936.8.26: 342–351); B, *Merluccius merluccius*, (1971.7.21: 44–57); C, *Lepidion eques*, (1984.3.21: 1–25); D, *Steindachneria argentea*, (1963.2.25: 335–9); E, *Gadus macrocephalus* (1984.12.5: 30–5). Outlines of posttemporal and posterior boundary of the epioccipital are indicated by dashed lines; the RLA nerve is shown as solid black but where covered by muscles is indicated by dotted line.

morphology, *Macruronus* possesses no such feature and its lateral ethmoid appears merely to be a derived modification of the plesiomorphic, rather than of the gadid, type.

3. Hyomandibular with lateral shelf

A lateral flange of the hyomandibular is not an uncommon feature among teleosts and, in itself, is probably plesiomorphic. However, a group of gadoids including *Merluccius*, Gadidae, Phycidae (part) and Lotidae possess a long, broad lateral shelf from which originates the inner part of the adductor musculature. In *Merluccius* the flange slopes ventrally and is prolonged by two processes, named by Inada (1981: 78) the intermuscular and preopercular (p. 88). No other gadoid taxa possess such a hyomandibular feature and it considered synapomorphic for the four (Figs 14A & B).

DISCUSSION

Regan (1903) noted 'The extreme interest of the genus *Macruronus*. . . has not yet been appreciated'. That appreciation is now realised through this study in which it is demonstrated that *Macruronus* exhibits features which question earlier concepts of gadoid phylogenetic relationships.

Relationships of *Macruronus* with *Lyconus* and *Lyconodes*

Following Norman's (1966) classification, Marshall's (1966) recognition of relationship between *Macruronus*, *Lyconus*, *Lyconodes* and *Merluccius* has not been seriously challenged (although Marshall, 1973, placed *Macruronus* and *Lyconus* as family *incertae sedis*). Cohen (1984) noted that '*Macruronus* is basically a *Merluccius* with a much reduced caudal fin', and that '*Lyconus*. . . is probably related to *Merluccius*'. On the contrary it seems that *Lyconus* and *Macruronus* are closely related and are phylogenetically widely separated from *Merluccius*.

Günther (1887) established the family Lyconidae to contain the genus *Lyconus* known then from a single small specimen, named as *L. pinnatus* collected in the South Atlantic. Subsequently, Holt & Byrne (1906) described a second species, *L. brachycolus* also based on a single specimen from the northeastern Atlantic. Brauer (1912) recorded three other small specimens of *L. pinnatus* from the Indian Ocean.

Lyconodes was described by Gilchrist (1922) from a single specimen and distinguished from *Lyconus* by its lack of anterior canine teeth, prolonged anterior dorsal rays and in having the gill-membranes united at the isthmus.

I have examined the type specimens of both *Lyconus* species but have not seen that of *Lyconodes*. The *Lyconus* types are both in poor condition, lacking their tail region and

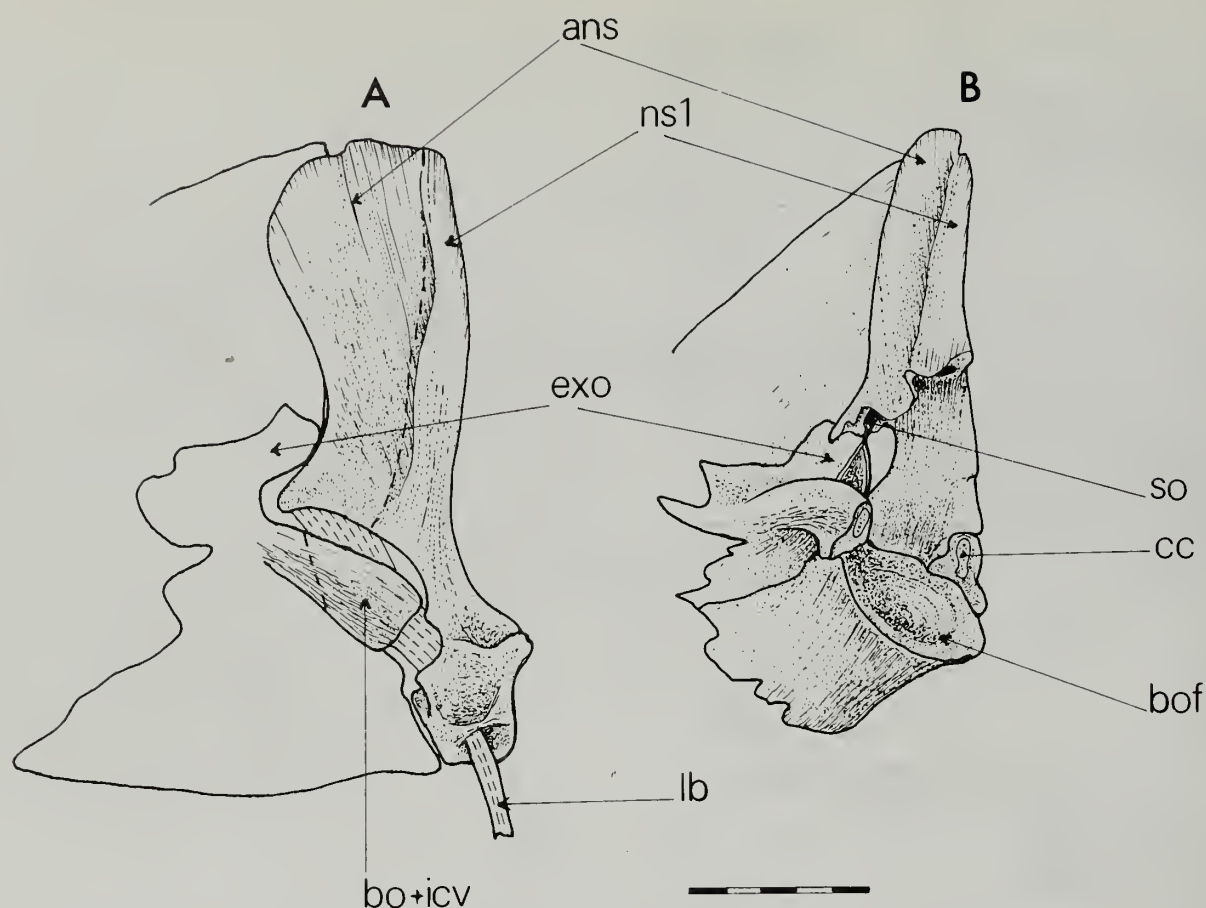


Fig. 29 *Macruronus magellanicus*, relationship of cranium and anterior vertebral elements. A, lateral view; B, ventrolateral view in which 1st centrum and lower part of left side of neural spine have been removed (BMNH 1936.8.26: 352-7, skeleton).

having damaged fins. The type of *L. pinnatus* is in very poor condition, having damaged jaws (Fig. 33). *Lyconus pinnatus* differs from *L. brachycolus* in having long, slender gill-rakers along the outer side of the first gill-arch (4 on the epibranchial + 12 on the ceratobranchial), whereas those in *L. brachycolus* are short, flat and have spinous dorsomedial surfaces. In this respect, *L. pinnatus* resembles *Macruronus*. According to Günther's (1887) description, *L. pinnatus* has a single canine-like tooth either side of the vomer (the teeth have now disappeared but their sockets remain visible); *L. brachycolus* has five and *Macruronus magellanicus* 6 or 7, and *M. novaezelandiae* 12 or more. The origin of the pelvic fins in both *L. pinnatus* and *Macruronus* lie beneath that of the pectorals, whereas in *L. brachycolus* (and *Lyconodes*) they are set forward.

Radiographs of both *Lyconus* species indicate a similar cranial morphology to that of *Macruronus*. In *L. pinnatus* the dorsal fin rays are broken off at their bases and externally it is impossible to distinguish two separate dorsal fins. The radiographs show, however, that there is a distinct gap between the 10th and 11th radial, which corresponds to the interdorsal space of *Macruronus*. For *L. brachycolus* a radiograph does not reveal such a gap, indeed, the 9th and 10th dorsal radials are closer together than are the others, but Holt & Byrne (1906) noted an inflection of the dorsal fin outline at the 10th dorsal ray.

Although *Lyconus* is said to have the gill membranes free from the isthmus, it appears that in *L. brachycolus* there is such a connection judging from the remains of membrane attaching to the isthmus, but that it has been torn away. Thus, although *Lyconus pinnatus* differs from *Lyconodes* in this respect, *L. brachycolus* does not and it fails as a feature distinguishing the two genera.

Lyconus brachycolus (Fig. 34) possesses apomorphies shared with *Macruronus*, namely an elongate anterior extension of the retroarticular, an enclosed sensory canal on the 5th infraorbital and a deep autosphenotic notch which accommodates the dermosphenotic (Fig. 33). I have been unable to determine whether *L. pinnatus* possesses the elongate retroarticular, but it certainly has a similar infraorbital and sphenotic morphology to *Macruronus*. *Lyconus pinnatus* differs from *Macruronus* only in the lower number of jaw teeth and seems to represent a juvenile specimen of that genus but on the available evidence is impossible to say to which species of *Macruronus* it belongs (p. 108).

Lyconus brachycolus differs from *Macruronus* in having a single dorsal fin and a more anterior position of the pelvic fin origin, features in which it appears to be the more derived taxon. In view of the apomorphies shared only with *Macruronus* it must be regarded as the sister taxon of that genus.

The phylogenetic position of *Lyconodes* cannot at present be determined. It too shows juvenile features in its extended pectoral fin rays (the type is only 45mm TL). Marshall (1966) has pointed out the posterior position of its pelvic fin in relation to the pectoral fin origin, and if it were not for this feature I would regard it as a juvenile of *Lyconus brachycolus*.

Recognition of *Lyconus* as a synonym of *Macruronus*, of *Lyconus brachycolus* as a distinct taxon, and the lack of close phylogenetic affinity of these taxa with *Merluccius* requires:

1. establishment of a new genus group name for *Lyconus brachycolus*.
2. recognition of a separate family to contain that taxon and its sister group, *Macruronus*.

In order to recognise *Lyconus brachycolus* as a distinct taxon

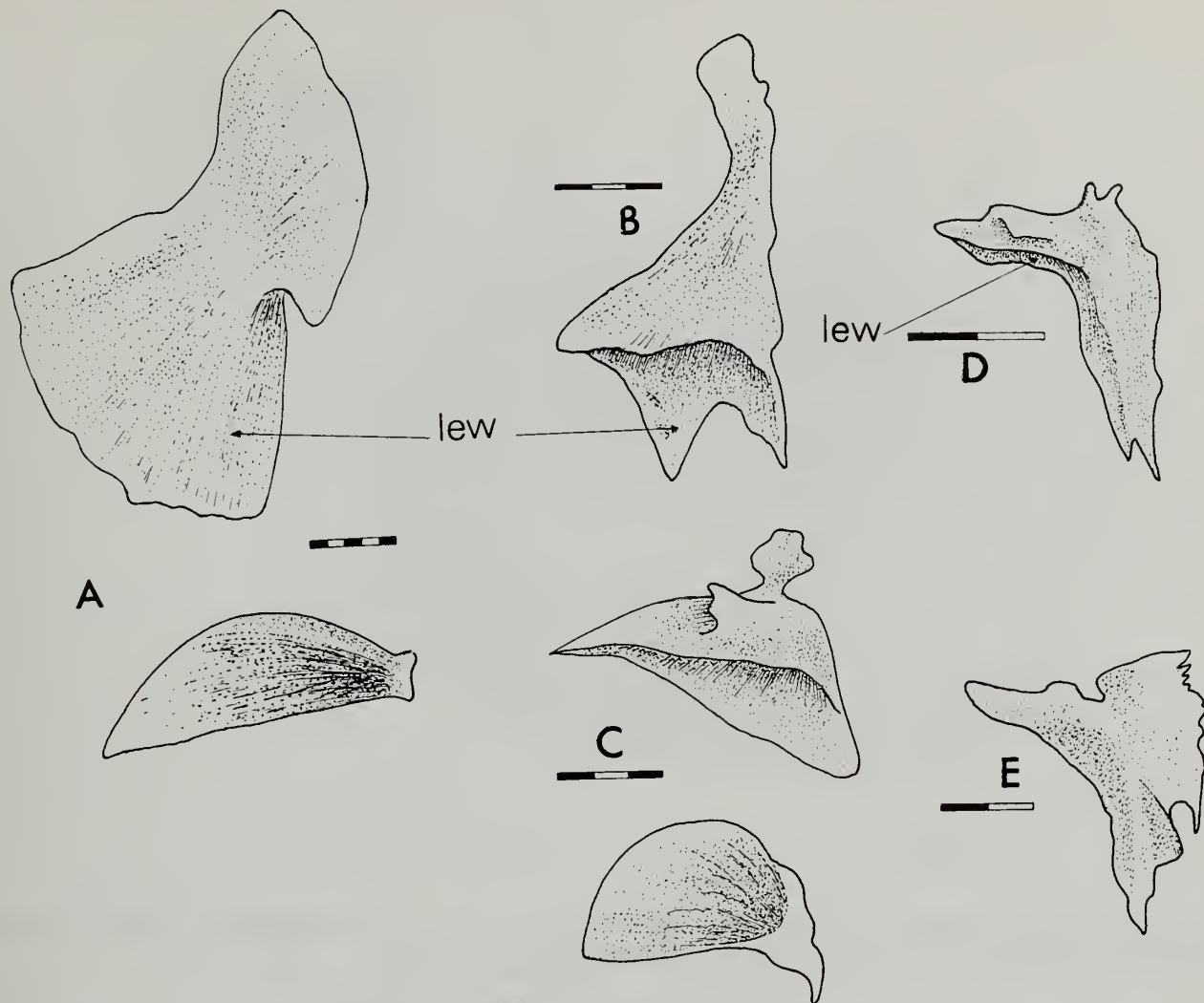


Fig. 30 Lateral ethmoids of; A, *Merluccius merluccius* in ventral and posterior views; B, *Gaidropsarus vulgaris*, ventral view; C, *Trisopterus luscus*, in ventral and posterior views; D, *Ciliata mustela* and E, *Raniceps raninus*, both ventral views (all unregistered skeletal specimens from the Ford Collection).

and sister group to *Macruronus* one may either expand the latter genus in order to contain it simply as another species, or emphasise its anatomical distinctiveness by recognising it as a subgenus or genus. This decision is a matter of opinion since at present there is no rigorous cladistic analysis of all gadoid families, i.e. no nested subsets by which one may judge the 'taxonomic-level' of a particular lineage. Rather than proliferate an already unstable classificatory system with more higher-level categories I have opted to recognise *Lyconus brachycolus* as representing a subgenus of *Macruronus*, referred to as *CYNOGADUS*, both for its characteristic canine teeth and for its overall resemblance to its macrouroid 'counterpart' *Cynomacrus* (see Appendix, p. 108).

Recognition of a separate family to contain *Macruronus* is taxonomically justifiable and necessary in order to indicate the relationships of *Macruronus* to other gadoids. Norman (1966) had already provided a family name, then recognised as a subfamily of the Merlucciidae, and here referred to as the MACRURONIDAE.

The relationships of the Macruronidae to other gadoids form the remainder of this discussion.

Relationships of the Macruronidae with other gadoid families

Knowledge of gadoid interrelationships is poor, indeed, even the recognition of higher taxa as subfamilies or families is based on the opinion of each author rather than a consensus

arrived at by employing rigorous methods of comparative analysis (see for example, Markle, 1982; Cohen, 1984).

Howes (1989) attempted to recognise lineages, ranked as families and recognised primarily on the basis of myological characters. Markle (1989) too has attempted a cladistic analysis based on a wider range of anatomical, but mostly osteological, characters. Both Markle's and my cladograms include unresolved polychotomies and suffer through lack of anatomical data and knowledge of character polarity. That said, our views of family relationships are not so radically different. For example, we both regarded the Moridae and Steindachneriidae as being closely related, the Muraenolepididae and Phycidae as being part of the same major group, and the Gadidae and Lotidae as belonging to a more derived lineage. We differed, however, in our view of the relationship of the Merlucciidae. Markle recognised it as the sister-group to the Gadidae and Lotidae while I placed it as the sister taxon to a group comprising five families within a broader complex termed 'higher gadoids'. (This category was recognised on the basis of a medial shift of the entire *adductor mandibulae* muscle A1b and loss of a palatine-lateral ethmoid ligament.) Nonetheless, both Markle and I, in common with other authors, recognised the Merlucciidae as a monophyletic lineage. My dispute with that supposition now leads me to reevaluate the phylogenetic positions of the Merlucciidae (now including the single extant genus *Merluccius*) and establish that of the Macruronidae.

Merluccius clearly belongs to the complex of 'higher

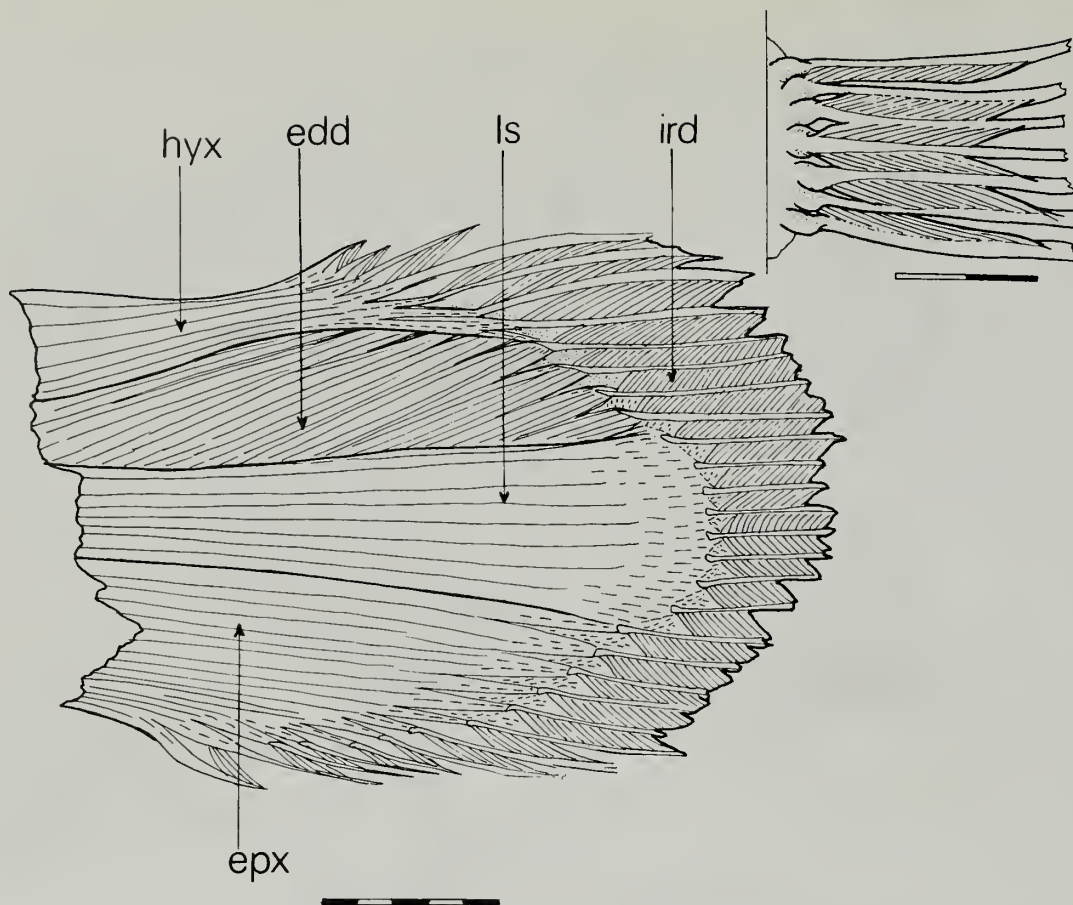


Fig. 31 Caudal fin musculature of *Urophycis regia* (BMNH 1985. 6.6: 109–119) showing superficial layers. Above, right, *interradialis* connection between medial caudal fin rays of *Gadus macrocephalus* (BMNH 1984.12.5: 30–33).

gadoids' in possessing a derived arrangement of the *adductor mandibulae* musculature (Howes, 1988), a well-developed articular facet on the interoperculum for the interhyal (p. 99) and a firm articulation between the dorsal process of the first infraorbital and the posterior face of the lateral ethmoid (p. 84). *Merluccius* also shares with the Gadidae, Lotidae and some Phycidae a strong lateral flange of the hyomandibular from which originates part of the *adductor mandibulae* musculature (p. 101), and shares a cone-shaped lateral ethmoid wing with the Lotidae and Phycidae. *Merluccius* also shares with phycids, gadids and lotids the tendency of attrition of the anterior wall of the prootic so that the trigeminal foramen is eroded into a notch. Only with the Gadidae does *Merluccius* share a medial prootic shelf (p. 98).

The Macruronidae lacks all of these 'higher gadoid' features and although specialized in many respects, has a generally low-level gadoid morphotype. In its caudal fin skeleton, the Macruronidae is hardly different from the Euclichthyidae, except that X and Y bones are lacking. Their absence is one the Macruronidae shares with the Melanonidae, Gadidae and Lotidae. Since the absence of 'higher gadoid' synapomorphies exclude a close relationship between the two latter families, the loss would appear to be an independent one. Likewise, there are no other identified synapomorphies that suggest a close relationship between the Melanonidae and Macruronidae.

The melanonid caudal skeleton is shown by Paulin (1983: fig. 5a) to possess, what I interpret (the figure is not labelled) as an autogenous parhypural; fused first and second hypurals; a compound centrum bearing lower hypurals separated from the upper, and two epurals. The separation of the upper hypurals (which I have not been able to confirm in the

specimen to hand) suggests a more primitive organization of the caudal skeleton than in *Macruronus*, and one not far removed from the Moridae in which all the upper hypurals are separated distally. I have not found in the Melanonidae, the connection of *interradialis* muscles between the caudal fin and dorsal and anal fins.

The Macruronidae shares no detectable synapomorphies with the Steindachneriidae, whose phylogenetic position is ambiguous. The Steindachneriidae lacks a caudal fin skeleton; has a primitive connection of the palatine with the lateral ethmoid wing and a primitive jaw muscle morphotype (Howes, 1987; 1988).

Contact of the palatine with the mesethmoidal portion of the lateral ethmoid (Howes, 1987) and complexity of jaw adductor musculature places the Macruronidae amongst the majority of gadoid families and its possession of a caudal skeleton having complete fusion of the upper hypurals into a single plate places it at a higher level of morphological specialization than Moridae and Euclichthyidae.

Euclichthyidae and Bregmacerotidae were considered by Howes (1988) as members of the 'higher gadoids'. However, re-examination of these taxa shows that an interopercular-interhyal joint is absent in *Bregmaceros* and only a shallow interopercular fossa is present in *Euclichthys*. *Bregmaceros* has, according to Markle (1982) attained the greatest internal and external caudal symmetry among gadoids. The relationships of the Bregmacerotidae are unclear and are positioned on the accompanying cladogram (Fig. 35) on the strength of a single character, namely, absence of a palatine-lateral ethmoid ligament, but this has been found subsequently in some 'higher gadoid' species.

As expressed here (and indicated by Rosen & Patterson,

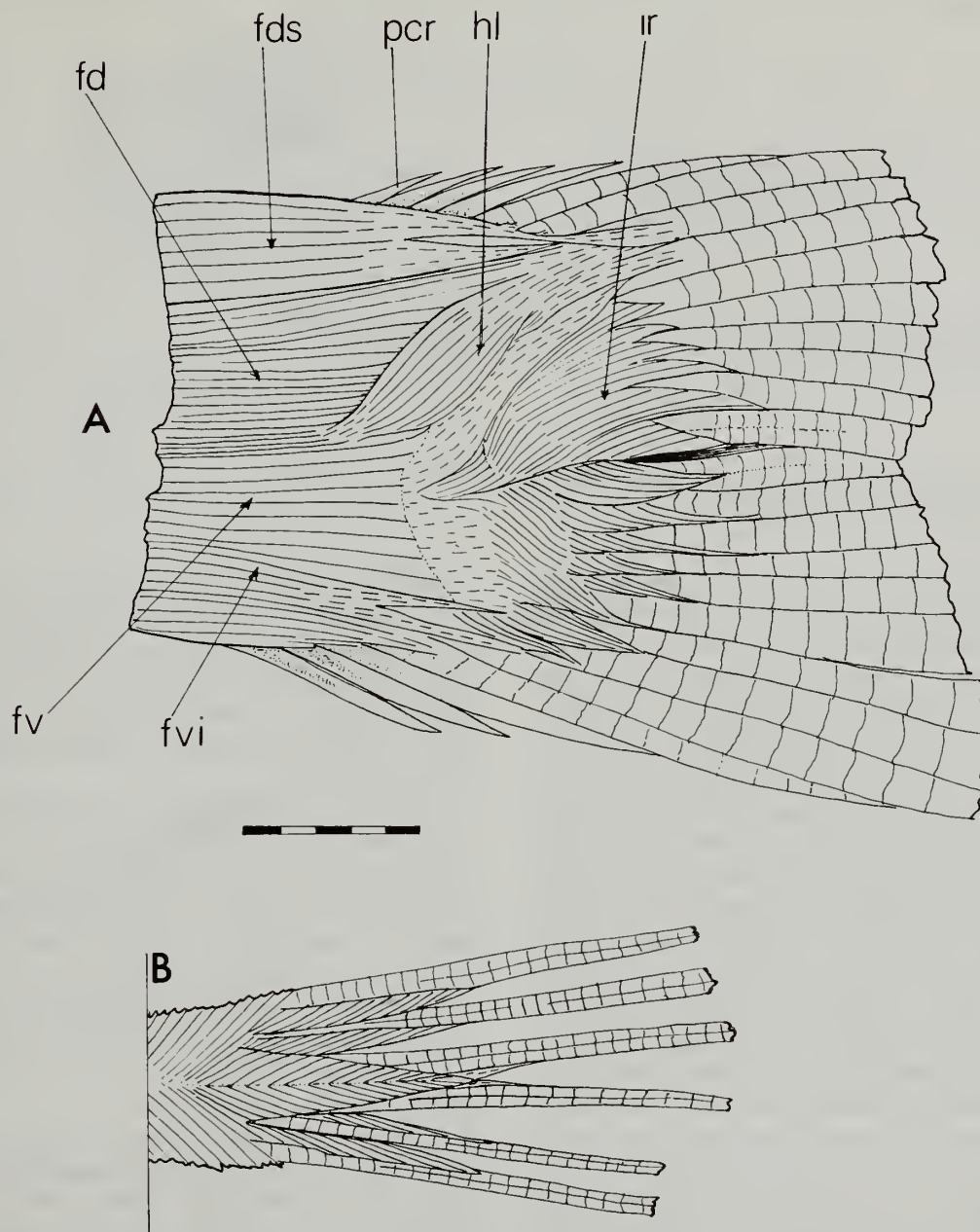


Fig. 32 Caudal fin musculature of; A, *Polymixia lowei* (BMNH 1987.12.7: 1-5); B, *Percichthys trucha* (BMNH 1935.4.23: 21-33), showing *interradialis* connections between medial caudal fin rays.

1969) the relationships of the gadoid families demonstrate a trend toward caudal fin element reduction by fusion that has been accompanied by re-organization and reduction of caudal fin musculature.

In gadoids the muscles serving the caudal fin are 'reduced' and simplified compared with those in most other teleosts. Symmons (1979) pointed out that in *Gadus* hypochordal muscles are lacking and that there are no intrinsic muscles associated with the vertebrae and caudal fin rays other than what she termed a pair of deep dorsal and ventral flexores (which I have referred to as a hypural segment of hypaxial muscle, there being only a dorsal and no ventral component; p. 94). Neither is there a superficial part of the *interradialis*, a feature common in other teleosts where a sheet of superficial fibres crosses the bases or necks of the caudal rays and so interconnects widely spaced rays. Among some acanthopterygians the *interradialis* is often thickened and complex and deeply divided between the upper and lower caudal lobes (see below). In gadoids the *interradiales* connect only one ray with another and the demarcation between upper and lower regions of the fin is marked by a change of direction of muscle fibres (see above and Fig. 27). Furthermore, *interradialis*

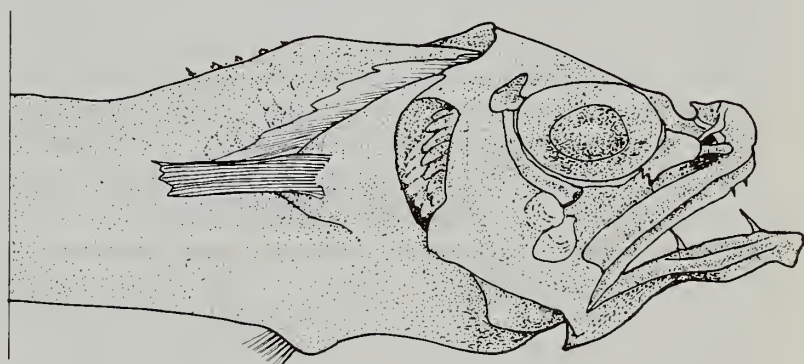


Fig. 33 *Macruronus (Macruronus) pinnatus*. Holotype, (BMNH 1876.3.4: 74). Lateral view of head and anterior body region. NB. Jaws and infraorbitals damaged and anterodorsal part of body torn.

muscles occur between the so-called procurrent caudal rays. They are absent between those rays in other teleosts.

The longitudinal dorsal and ventral muscles attaching to the upper and lower caudal rays represent what I believe to be merely epaxial and hypaxial muscle bands and are thus not

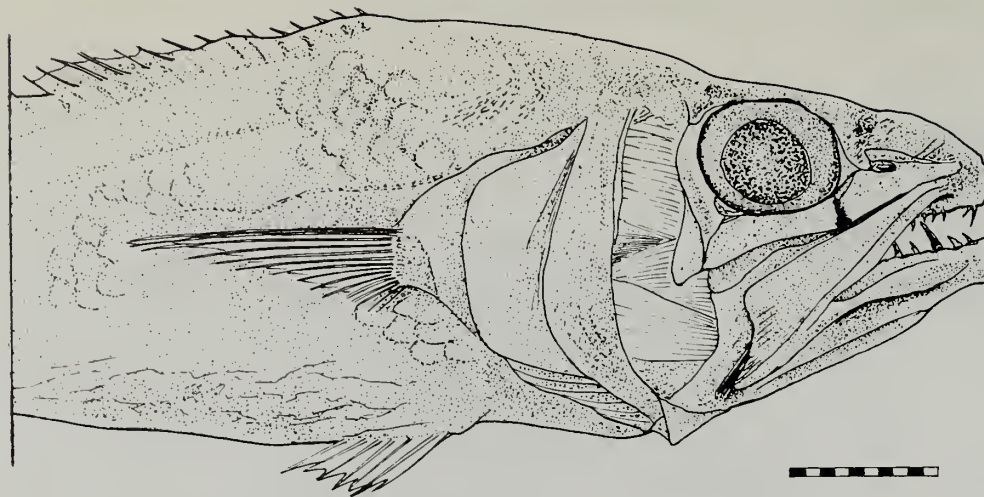


Fig. 34 *Macruronus (Cynogadus) brachycolus*. Holotype, (BMNH 1907.6.20: 15). Lateral view of head and anterior body region. NB. Infraorbitals damaged and head partially dissected.

homologous with the *flexores dorsales* and *ventrales* of other teleosts (Fig. 32). Likewise, the posterior segment running from the terminal centrum (hypural plate) and inserting on the upper caudal ray bases does not appear to be the homologue of the *hypochordal longitudinalis* of other teleosts. That muscle, in acanthopterygians at least, is separated from the *interradialis* by a hypural marginal area of thick collagenous tissue covering the bases of the caudal rays. The *hypochordal longitudinalis* in other teleosts has a long base which usually originates from a hypurapophysis, and narrows at its points of insertion. The analogous muscle segment in gadoids has a short area of origin on the anterodorsal area of the terminal centrum and broadens over its area of insertion (see Fig. 27A). Macrouroids (including *Trachyrincus*) possess a body muscle morphology similar to that of gadoids except that there is no separately identifiable posterior segment attaching to the hypural plate; the upper and lower longitudinal muscle bands connect with caudal rays.

Differences between the arrangement of the caudal fin musculature in gadoids and other investigated teleosts signify a lack of homology between the elements. The absence of complex *interradiales*, the development of those muscles between 'procurrent' caudal rays, the absence of *flexores dorsales* and *ventrales*, and *hypochordal longitudinalis* all point to the modification of the caudal fin skeleton. I would suggest that '*interradiales*' muscles of gadoids are modified *depressores dorsales* and *ventrales* since they comprise two components and occur between the 'procurrent' rays.

The taxonomic significance of caudal fin musculature has so far been overlooked. For example, in acanthopterygians there are marked differences in how upper and lower caudal fin lobes are served by *interradiales* muscles. In *Polymixia*, which represents the majority of taxa reported upon (Winterbottom, 1974; Videler, 1975), division is complete, each lobe being controlled by different bundles of *interradiales* (Fig. 32A). In *Percichthys*, however, the medial rays of upper and lower lobes are connected by a single, pinnate muscle whose oppositely directed fibres are joined in a midline raphe (Fig. 32B). These and other features require a full investigation from taxonomic, phylogenetic and functional standpoints.

Complete loss of a caudal skeleton is characteristic of two gadoid families, Bathygadidae and Steindachneriidae, as well as of the Macrouroidei. In Trachyrincidae, the caudal skeleton is modified by apparent loss of various elements and

a 'gadoid symmetry' is ambiguous (Howes, 1989). In its rat-tailed appearance, reduced upper hypural plate and loss of X and Y bones it is tempting to regard the Macrouroidei as representing an evolutionary condition tending toward total caudal loss. Boulenger (1902) and Regan (1903) considered the gadoid caudal skeleton to be a *de novo* development from a tailless state.

If Fahay's (1989) hypothesis that Steindachneriidae is the plesiomorphic sister group of Macrouroidei, and Howes & Crimmen's (1990) suggestion that Bathygadidae is the plesiomorphic lineage of other gadiforms be accepted, then serious consideration must be given to Boulenger's and Regan's suggestions. There is, however, no comparative anatomical or ontogenetic evidence that would suggest *de novo* development and it is assumed that caudal skeleton loss has been independently derived in those various lineages (Howes & Crimmen, 1990).

To summarise; the Macrouroidei forms the sister-group to a lineage comprising Bregmacerotidae, Muraenolepididae, Ranicipitidae, Phycidae, Lotidae, Gadidae and Merlucciidae (Fig. 35). Relationships of these families to one another remain to be more completely resolved as do those of the 'lower' gadoids, Melanonidae, Steindachneriidae and Bathygadidae.

Concerning the Eocene merlucciid *Rhinocephalus*, this fish appears correctly assigned to this family. The pattern of frontal crests, infraorbital morphology and arrangement of otic bones, including an aperture bounded by the prootic and pterosphenoid for the trigeminal nerve tract, all indicate its merlucciid affinity. Although the caudal skeleton of *Rhinocephalus* is unknown, those of other Eocene gadoids resemble morids (Rosen & Patterson, 1969: 432-3). If *Rhinocephalus* proves to have an advanced gadoid caudal skeleton (as in *Merluccius*) then it would suggest that the division between 'lower' and 'higher' gadoids would have been established by the Eocene.

ADDENDUM

After this paper had been accepted for publication, two papers appeared which contain phylogenetic relationship hypotheses of *Macruronus*. Both Okamura (1989) and Inada (1989) treat *Macruronus* and *Lyconus* as a sister group to

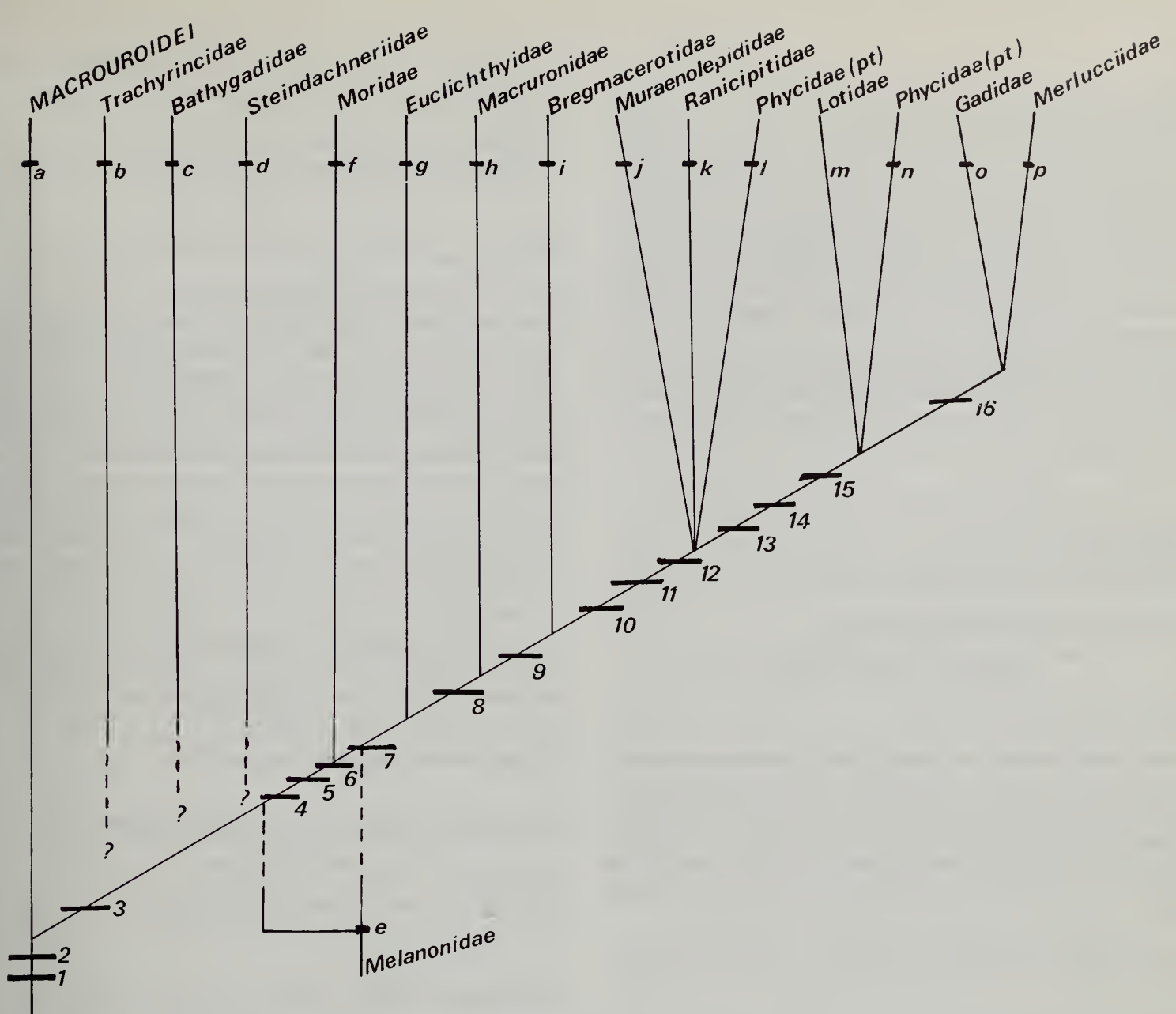


Fig. 35 Cladogram of gadoid relationships. Synapomorphies relating families: **1**, *Levator arcus palatini* muscle lies lateral to *adductor mandibulae*; **2**, Absence of pars jugularis (a single opening serves for the transmission of all cranial nerves and vessels); **3**, *Rectus communis* muscles attached to *sternohyoideus*; **4**, X and Y bones in caudal skeleton (lost in Melanonidae, Macruronidae, Lotidae and Gadidae; presumably also in Trachyrincidae, Bathygadidae and Steindachneriidae); **5**, Caudal fin muscles modified, *interradiales* connect caudal fin rays with dorsal and anal rays; **6**, Palatine contacts the mesethmoidal part of lateral ethmoid; **7**, Medial shift of muscle A1b; **8**, Complete fusion of upper hypurals into single plate. (According to Markle (in litt.) upper hypural plate of *Raniceps* is bifurcate and ontogenetically displays more than two upper hypurals). This demonstration of ontogenetic fusion could thus be considered a character reversal; distribution of other synapomorphies do not support the view that *Raniceps* occurs at a lower phylogenetic level; **9**, Loss of lateral ethmoid-palatine ligaments; **10**, 1st infraorbital contacts posterior face of lateral ethmoid wing; **11**, Posterohyal articulates with an interopercular fossa whose rim forms a 'stop' to its posterior movement; **12**, *Rectus dorsalis* muscle inserts on pharyngobranchial 4 in addition to 3 (exceptions: *Merluccius*, inserts only on 3; *Muraenolepis*, inserts only on 4); **13**, Hyomandibular with lateral shelf; **14**, Cone-shaped lateral ethmoid wing; **15**, Attrition of the prootic anterior border with often, in conjunction with pterosphenoid; formation of separate foramen for trigeminal and hyomandibularis nerves; **16**, Medial prootic shelf.

Synapomorphies for lineages: **a**, Macrouroidei; loss of interopercular-subopercular ligament; many other synapomorphies, discussed in Howes & Crimmen, 1990; **b**, Trachyrincidae; *Adductor mandibulae* A1 muscle a single element, nasal bones extended, palatine immobile (Howes, 1987, 1988; 1989), caudal fin skeleton 'rudimentary' (Howes, 1988b and this text); **c**, Bathygadidae; pectoral branch of RLA nerve hypertrophied (Howes & Crimmen, 1990); **d**, Steindachneriidae; luminescent organs, wide separation between anus and urogenital opening, enlarged anal radial and compound first anal fin ray (Fahay, 1989); **e**, Melanonidae; specialized neuromast pattern, ectopterygoid teeth, loss of *intermandibularis* muscle; **f**, Moridae; primitive otophysic connection (Paulin, 1983), swimbladder with horizontal septum (Paulin, 1988), parasphenoid with transversely aligned ascending process (this text); **g**, Euclichthyidae; jugular placed and reduced pelvic girdle, pelvic rays and anterior rays of anal fin extended, lateral ethmoid wing transversely convex; **h**, Macruronidae; retroarticular with anteroventral prolongation, prootics form a wall across the midline, modified caudal fin skeleton, modified infraorbital bones, *adductor arcus palatini* muscles originates partly from a ventral palatine fossa (this text); **i**, Bregmacerotidae; single first dorsal fin ray articulating with an angled radial lying along the supraoccipital crest, advanced symmetry of the caudal fin (Markle, 1982) reduced metapterygoid and operculum (pers. obs.) *adductor mandibulae* muscle reduced to a single element (Howes, 1988); **j**, Muraenolepididae; derived palatine morphology (Howes, 1987), *rectus dorsalis* muscle inserts only on pharyngobranchial 4 (Howes, 1988); **k**, Ranicipitidae; first dorsal fin with 3 rays, lateral line reduced; **l**, Phycidae (*Phycis*, *Urophycis*) *epaxialis* muscle inserts on operculum (also shared with the *Muraenolepis* and *Lota*), frontals fused (shared with Gadidae), anterior diverticulum of swimbladder adnate to exoccipital (pers. obs.); **m**, Lotidae, no well corroborated synapomorphies for *Molva*, *Lota* and *Brosme*, those given by Markle, 1982 are, absence of pterotic spine, initial pelvic fin ray formation prior to flexion, and delayed acquisition of adult complement; **n**, Phycidae (*Gaidropsarus*, *Motella*, *Ciliata*, *Rhinonemus*), first dorsal fin comprised of several filamentous rays contained in a dorsal groove, and supported by modified radials (Markle, 1982); **o**, Gadidae; three dorsal fins, reduced and enclosed 'mucous' cavity of the frontals, frontals fused in most taxa, swimbladder with elaborate anterior diverticulae; **p**, Merlucciidae; enlarged vertebral parapophyses, hyomandibular with two long, lateral ventrally directed processes, *levator arcus palatini* muscle originates from a lateral palatine fossa, medial prootic shelves form pseudo-posterior myodome (this text)

From this cladogram, it follows that the Gadoidei are embraced by character 3. Since, however, this feature is also encountered in some macrouroids (Howes, 1988a) its status as a synapomorphy is weakened. Alternatively, recognition of the Gadoidei by characters 5 and 6 places the Trachyrincidae, Bathygadidae, Steindachneriidae and Melanonidae as *incertae sedis*. This cladogram has since been superseded by another (Howes, 1990) in which the Muraenolepididae is aligned with the Lotidae and the second part of the Phycidae.

Merluccius. In other words, they accept the near-traditional view of the Merlucciidae (recognised as a family by Okamura and a subfamily by Inada. Both authors use characters which are regarded therein either as plesiomorphic or homoplastic. Inada's sole 'synapomorphy' for allying the three genera is the V-shaped frontal ridge, a feature discussed here and deemed plesiomorphic for gadoids. Okamura presents no evidence for grouping the three genera other than 'All characters are opposite, that is, primitive states of those of *Steindachneria*'.

I do not believe that either author has addressed the problem of merlucciid monophyly and none of the characters they present are new or are polarized through adequate out-group analysis.

APPENDIX

Taxonomy of the Macruronidae

Family MACRURONIDAE

Macruroninae Norman 1966:196

Distinguished from other gadoid families in arrangement of dentition, having large, compressed caniniform teeth in outer row of both jaws and an inner row of small, horizontally aligned and medially directed teeth; anteriorly extended anteroventral margin of retroarticular; densely ossified 5th infraorbital and reduced 6th contained in a sphenotic-frontal notch.

TWO GENERA: *Macruronus* Günther, 1873; *Lyconodes* Gilchrist, 1922.

Macruronus

Günther, 1873: 103; type species *Coryphaenoides novaezelandiae* Hector 1889: 196

Lyconus Günther, 1887: 158; type species *Lyconus pinnatus* Günther, 1887: 158.

Subgenera: *Macruronus*; *Cynogadus* (p. 103).

Species:

Macruronus (Macruronus) novaezelandiae (Hector, 1889)

Coryphaenoides novae-zelandiae Hector, 1889: 157

Macruronus novae-zelandiae Günther, 1873: 103; 1887: 157

For description, see Waite, 1911: 180, and for bioeconomic data, Kuo & Tanaka, 1984a,b,c. and Patchell, 1982; for larval development, Patchell *et al.*, 1987; Bruce, 1988.

DISTRIBUTION: New Zealand, Tasmania.

Macruronous (Macruronus) magellanicus Lönnberg, 1907

Macruronus magellanicus Lönnberg, 1907: 15

Macruronus novae-zelandiae (non Hector) Günther, 1880: 22

Macruronus argentinae Lahille, 1915: 22

For description, see Norman (1937:49) and Inada (1986), and

for bioeconomic data, Hart (1946) and Torno & Tomo (1980).

DISTRIBUTION: coastal areas and banks off southern South America.

Macruronus (Macruronus) capensis Davies, 1950

Macruronus capensis Davies, 1950: 512

Described from a single specimen, Davies distinguished this from other species on the presence of a small 'spine' and 13 soft rays in the first dorsal fin. However, there is a reduced first ray present in all *Macruronus* species and there are 13 longer rays in *M. magellanicus*. Davies also noted a supposed difference in dentition, mistakenly believing that teeth were absent in the upper jaw of *M. magellanicus* and that two rows of upper jaw teeth were a feature unique to *M. novaezelandiae*. The inner row is, however, present in *M. magellanicus* and is visible only when tissue covering the inner surface of the jaw is removed (see Fig. 11C), and so it seems likely that Davies overlooked these teeth.

Davies also maintained that the locality (off the Cape) and depth of capture (280 fms) further signified 'specific distinctiveness'. Since Davies's description further specimens have been reported (Cohen, 1986: 325).

DISTRIBUTION: Off South African Cape.

Macruronus (Macruronus) caninus Maul, 1951

Macruronus caninus Maul, 1951: 45

Known from three specimens; provenance uncertain, but most likely the southern coast of Madeira.

Macruronus (Macruronus) maderensis Maul, 1951

Macruronus maderensis Maul, 1951: 49

Known from eight specimens, all juveniles (the largest 85mm TL), taken from the stomach of an *Alepisaurus ferox*; off Madeira.

Macruronus (Macruronus) pinnatus

Lyconus pinnatus Günther, 1887: 158.

The type (Fig. 33) and other known specimens are all juveniles. Recorded from the south Atlantic and Indian Oceans.

Macruronus (Cynogadus) brachycolus

Lyconus brachycolus Holt & Byrne, 1906: 424

Known only from a single specimen from the Irish continental shelf (Fig. 34).

The species of *Macruronus* are poorly known and the distinctions between them are slight. *Macruronus (M.) magellanicus* is distinguished from *M. novaezelandiae* on the basis of its smaller eye and longer premaxillary; the two species from Madeira supposedly have fewer rays in the first dorsal fin, both are described from juvenile specimens which may be conspecific with the southern Atlantic species. Only the collection and study of more material will determine whether the described taxa represent distinct species or populational variants of a single cosmopolitan one.

ACKNOWLEDGEMENTS. I am most grateful to Humphry Greenwood, Douglas Markle, Colin Patterson and Alwyne Wheeler for their critical readings of the manuscript and their many helpful comments. My thanks are also due to Patrick Campbell, Oliver Crimmen and Mandy Holloway for their many and varied technical services.

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Manuscript accepted for publication 8 March 1989